# Observations of the Reproductive Cycles and Ecology of the Common Brachyura and Crablike Anomura of Puget Sound, Washington

JENS W. KNUDSEN[1]

IT WAS THE AIM of this research project to study the growth and reproductive cycles of the Puget Sound Brachyura and Anomura as they are related to oceanographic and environmental conditions. These goals were designed to answer many of the basic questions concerning the local crab population and to serve as a basis for more restricted physiological experimentation dealing with behavior and reproductive cycles. A continuous survey of the intertidal and near-shore crab fauna was made to determine the seasonal change in gonad development, egg production, the time of fertilization, deposition of eggs, and other related features. As many species of Anomura and Brachyura as could be accommodated were captured and maintained in running sea water aquaria for additional studies of food and feeding habits, ecdysis, copulation, and other phenomena linked to maturity and reproduction. The aim to survey all Brachyura and Anomura in the southern Puget Sound area had to be modified to exclude the hermit crabs due to the extreme amount of time required for field observation of this group. It has been our goal to correlate reproductive activity of all of these species with annual environmental changes so far as possible and to determine trigger mechanisms involved in the reproductive cycles. Considerable experimentation was attempted along these lines as is discussed herein.

## ACKNOWLEDGMENTS

A research project of this nature has required the help and support of many institutions and individuals. To the Division of Biological Sciences of the National Science Foundation that has generously granted Pacific Lutheran University funds for this research,[2] the principal investigator and those students who received research experience and financial aid wish to express their thanks. The Metropolitan Park Board of Tacoma has rendered a tremendous service in providing research space at the Point Defiance Aquarium; we wish to thank them, and especially Cecil Brosseau, for their help with space, equipment, and invaluable information. We wish to acknowledge the special laboratory space and facility donated by Dr. S. C. Eastvold and the Pacific Lutheran University. The writer wishes to express his indebtedness to biology majors who have served on this project. Especially helpful have been the efforts of Bert Freeman and Lloyd Dillingham; in addition, other student assistants served one or more semesters on the grant: Ron Barbour, Ray Herbig, Gary Vestal, Ruth Olsen, Pat Lingelbach, and Ron Heyer. The art work was done by Ron Heyer. Of invaluable aid have been the suggestions and help rendered by other carcinologists, especially Dr. Josephine F. L. Hart Carl of the Provincial Museum, Victoria, British Columbia, and Dr. John S. Garth of the Allan Hancock Foundation, University of Southern California, Los Angeles.

## FIELD COLLECTING AND STUDY AREAS

Three main sites were used within the area of Tacoma for year-long study of the southern Puget Sound crabs. These sites are somewhat variable in nature and thus offer a good cross-section of the different types of habitat within Puget Sound. Collecting was confined to the intertidal area because adequate dredging facility was not available.

The most frequently visited site was that of Titlow Beach. This is a curved beach situated at the southern end of the Tacoma Narrows where the bay is fairly broad and is protected by pilings

[1] Department of Biology, Pacific Lutheran University, Tacoma 44, Washington.

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and ferry dock facilities at one end and a somewhat rocky prominence at the other end. Thus relatively calm water free from strong currents exists. The substrate grades from rocky rubble to almost pure mud. In one area a small stream drains into the Titlow Beach habitat and has formed an underwater delta consisting of mud and coarse sand. Along the upper margin of the beach large boulders have been placed as a retaining wall, thus affording a site where spray zone animals and plants may live. This beach is typical of most Puget Sound intertidal areas.

The second site studied was at the Point Defiance boathouse. Situated on the north side of Point Defiance, it opens to the Dalco Passage. The immediate area associated with the boathouse is similar to that of Titlow Beach, for rock rubble covers much of the shell-fragment and coarse sand substrate. Adjacent to the boathouse, however, a long expanse of beach extends toward the north and west and affords a heavy growth of *Zostera marina*. At this site those species that dwell typically on pilings or under rock rubble or within the *Zostera* beds were studied.

The third site frequently visited was under the Narrows Bridge in that confined stretch of water known as the Tacoma Narrows. This is the only drainage site for the extremely large southern arm of Puget Sound and hence the currents "boil" through the Narrows at a high velocity during the changing of the tide. On the east side of the Narrows very large boulders have been placed by the railroad company to retain the banks. A limited number of very narrow beaches extend out from these boulders. From the low low-water mark the substrate frequently drops off abruptly to depths that appear to be 15 ft or more. This habitat is so heavily washed by swift currents that sediments not protected by rocks are swept away. Those animal and plant species that fully require a protected outer rocky coast with fairly strong oceanic waves often exist here because the high velocity of the current serves as a substitute for waves. This site was visited whenever the tides were sufficiently low to insure good collecting.

Three other sites were visited on occasion. Gig Harbor, just north of Tacoma, is a well-protected area with a muddy bottom and a large number of piers and floating boat docks. This site was examined occasionally for the large number of spider crabs that could be found there. Quartermaster Harbor across from the Point Defiance Aquarium offered a large number of piers for collecting. Another site visited three or four times annually was near the lighthouse in the Port Orchard channel just north of Port Orchard, about 1 mile southwest of Point Glover and across the channel from White Point. The prominence at the lighthouse is a natural headland composed of very large boulders that project out into the waterway. Like the Narrows, this site has extremely heavy currents; unlike the Narrows, however, the rocks project straight out into the current rather than simply forming a margin along the current. This site was well provided with invertebrates, some of which are found almost exclusively in the outer reaches of Puget Sound or in the protected open oceanic coastline. Likewise the flora was more reminiscent of that of the protected rocky coastline. Here many of the species of crabs that had been encountered in southern Puget Sound were also present, but in addition such genera as *Pachycheles* were found.

## METHODS AND MATERIALS

FIELD COLLECTING: The tide in the eastern Pacific is a mixed tide, thus giving unequal lows or highs during any given day. About every 14 days a period of low tides occurred but only once out of each month would the tide be sufficiently low to enable the collection of specimens which live at the extreme lower limits of the intertidal zone. Several collecting trips were made during each series of low tides. During the transitional periods of tidal change (January–March and September–October) bimonthly collecting was continued and an endeavor was made to obtain all of those species under study, even though the depth of the tides was not adequate. However, it was necessary to use laboratory animals in part to fill in where field records were not obtainable. In many instances it was felt that the laboratory data were not obtained under natural conditions and thus these have been disregarded in the final analysis. Collecting was always carried out by hand or by hand-operated nets and dredges.

LABORATORY FACILITIES: The Pacific Lutheran University facility consisted of a very large walk-in cooler with a system that maintained room temperature isothermally with Puget Sound water. Aerated glass aquaria filled with sea water were set up in this cold room. The room was partitioned off with a completely light-proof curtain, and independent lighting systems with time clock controls were set up on either side of the room. Aquarium heaters were employed when higher than room temperatures were desired. Thus it was possible to control the length of "daylight" and the tank temperature so that many environmental factors could be altered within each aquarium.

The Point Defiance facility consisted of nine

BRACHYURA AND CRABLIKE ANOMURA OF SOUTHERN PUGET SOUND
(List Not Complete)

| Species | Remarks |
|---|---|
| **Brachyura-Grapsidae** | |
| *Hemigrapsus nudus* (Dana) | Very common. |
| *Hemigrapsus oregonensis* (Dana) | Very common. |
| **Xanthidae** | |
| *Lophopanopeus bellus bellus* (Stimpson) | Common. |
| **Cancridae** | |
| *Cancer productus* Randall | Common. |
| *Cancer magister* Dana | |
| *Cancer gracilis* Dana | |
| *Cancer oregonensis* (Dana) | Common. |
| *Telmessus cheiragonus* (Tilesius) | At Titlow Beach, rare. |
| **Majidae** | |
| *Chionectes bairdi* Rathbun | University of Puget Sound, dredged 18 fathoms. |
| *Hyas lyratus* Dana | University of Puget Sound collection, dredged. |
| *Oregonia gracilis* Dana | Not numerous. |
| *Pugettia gracilis* Dana | Common, but not numerous. |
| *Pugettia producta* (Randall) | Common, but not numerous. |
| *Scyra acutifrons* Dana | Common, but not numerous. |
| **Anomura-Porcellanidae** | |
| *Petrolisthes eriomerus* Stimpson | Abundant in restricted localities. |
| *Pachycheles rudis* Stimpson | Not abundant. |
| *Pachycheles pubescens* | Not abundant. |
| **Lithodidae** | |
| *Cryptolithodes typicus* Brandt | One specimen, Tacoma Narrows. |
| *Haplogaster mertensii* Brandt | Not common, restricted. |
| *Lopholithodes foraminatus* (Stimpson) | Dredged by Point Defiance Aquarium. |
| *Phyllolithodes papillosus* Brandy | Very rare. |

30-gal aquaria of a plywood construction, one 150-gal tank, and numerous smaller aquaria. All of these were supplied with running sea water and furnished with both barnacle-encrusted rocks and marine algae as required by the different species of crabs. A time switch controlled the lighting so that the length of "daylight" could be regulated. Different species of crabs were seldom mixed within the various tanks, to avoid competition and fighting. The cleaning of the tanks and feeding of the crabs twice weekly demanded the full-time attention of one student throughout the entire project.

REPRODUCTIVE CYCLE: Almost all of the data collected concerning the annual reproductive cycle of the various species studied were obtained by field collecting, and only where an indication is made to the contrary are the data obtained by laboratory observation. By selecting and preserving samples of the crabs collected, the development of ova within the ovaries could be watched and measured. Ovaries were studied by dissecting these and placing them on a temporary wet-mount microscope slide. They were then placed on a micro-slide projector and the projected ovary with its developing ova was measured by a predetermined metric scale. Size and color data were recorded in each case.

Observations of crab copulation were made by chance. With the numerous field trips and continuous laboratory observation, many fine records were obtained. The crabs were at no time conditioned by hormones or isolated for copulation studies, and all records are considered to be normal and valid.

The time of egg deposition was obtained from the field record. As many females as possible or practical were collected bimonthly, and counts of the total number of females with eggs and studies of the egg condition were made. Incubation period is determined mainly from the total field record as plotted, or, from the literature. In few cases are the data obtained in the laboratory. In most instances it was felt that laboratory results may be altered somewhat due to some abnormal condition and therefore field records were used whenever possible. In some cases the actual mechanics of hatching were observed for various species of crabs. The number of broods per year was determined by field observations, laboratory observations, and by the dissection of females carrying developing eggs on the pleopods. These dissections determined the nature and degree of development within the ovaries. All three means were used whenever possible to give an accurate picture of the number of broods per year. Some attempts were made to study the larval development by actually rearing larvae in the laboratory. By far the largest proportion of crabs in Puget Sound have already been studied and the description of the larvae of these crabs is now being prepared for publication. Those species yet unstudied remain so because of difficulty in rearing them in the laboratory. Many species already known were run through the life cycles in part at least to compare both the morphology and ecology with the literature.

## FAMILY Grapsidae

*Hemigrapsus* HABITAT: The two species of *Hemigrapsus, nudus* and *oregonensis,* will be treated together for the sake of comparison. The habitat of *H. nudus* is listed by Way (1917: 358), as being a situation where rocks and stones cover a sandy substrate. MacKay (1931: 189; 1943:151), Rathbun (1918:268), and others simply list the habitat as being among rocks near shore. Schmitt (1921:274) describes *H. nudus* as being strictly a littoral species. Hiatt (1948:141) encountered *H. nudus* and *H. oregonensis* in what he calls "the second and less common biotope" of *Pachygrapsus crassipes.* This biotope is found most commonly in estuaries and bays, and consists of a gradation of very large boulders giving way to rock and stone and finally gravelly rubble as one proceeds from the offshore area towards the higher reaches of the intertidal zone. Hiatt mentions that *Pachygrapsus crassipes* is quite abundant around the larger boulders but is replaced by *H. nudus* and finally by *H. oregonensis* as one moves progressively toward the fine sandy or muddy substrate.

*Hemigrapsus oregonensis* is thought of as living on muddy portions of the coast line (Way, 1917:359; MacKay, 1943:152; and others). Hiatt (1948:142) lists this species as being common in the third biotope of *P. crassipes,* along muddy shores of bays and estuaries. He describes the hiding places of this species as small holes formed along mud banks, from which the crab will venture out to foray along the entire expanse of the muddy beach. Schmitt (1921:275) suggests that *H. oregonensis* is quite common in dredge hauls ranging from 1¼ to 3½ fathoms. The substrate from which these hauls were made consisted of shelly bottoms or mud bottoms.

Within the southern Puget Sound system of waterways one will encounter a variety of substrates beginning with large coarse boulders where the current is rather swift, such as the Port Orchard area or the Tacoma Narrows. Adjacent to this the substrate gives way to rock over sand where the boulder size may become progressively smaller, until finally one encounters in the numerous small bays and inlets a pure mud or fine sand substrate intermingled here and there with gravel in areas where seepage is quite common.

The substrate of coarse to fine sand overlain with a fair supply of rocks and boulders makes up the greatest expanse of the intertidal area. To a collector first visiting this type of a habitat it would appear as if the two species of *Hemigrapsus* share the identical habitat, for both abound in very large numbers. However, *H. nudus* prefers the upper reaches of the intertidal zone and is found abundantly during periods of low tide under large boulders situated over a coarse sand or broken shell substrate. Ricketts and Calvin (1952:208) note that *H. nudus* is found in a "middle zone" in California, where temperatures are cooler than in the upper zones, while it is found in the upper zone in Puget Sound. The temperatures in these two zones may approach being isothermal and thus explain the pattern of distribution. *H. oregonensis* is most common in the lower reaches of the intertidal zone. A careful check of the substrate will show that this crab is found where there is a very fine silty sand or mud present beneath the rocks, and that frequently coarse gravels make up a substrate between the rocks. This species seems to prefer shallow depressions where the gravel or mud is saturated with water, a sharp contrast to the very well-drained substrate on which *H. nudus* is often found. There are numerous invertebrate burrows in this habitat and these are frequently occupied by *H. oregonensis*. *H. nudus* also visits this lower zone from time to time, especially during the colder parts of the winter months when both sexes move down in the intertidal zone, or in the spring when females carrying eggs will occasionally be found hiding there. There are no data, however, which suggest that females move to this zone in order to keep the eggs moist, for equally large numbers are found at low tide in the very high and extremely dry parts of the intertidal area. When *H. oregonensis* is found in the uppermost reaches of the intertidal area, it is in situations which are kept moist by surface run-off or in depressions where very shallow tide pools form. Thus, the preference seems to be that *H. nudus* will select larger boulders with relatively good drainage beneath and that *H. oregonensis* will select any situation in which the body may be bathed almost continuously with water.

As one moves from this typical habitat to the more rocky headlands, he finds that *H. oregonensis* begins to drop out in population counts but that *H. nudus* remains a dominant member of the fauna. Conversely, as one moves from the rock and sand situation towards that of a fine mud and gravel, he finds that *H. nudus* drops from the population count but *H. oregonensis* becomes extremely abundant. This habitat is perhaps more suitable for *H. oregonensis* since, because of its diminutive size, this crab can hide even between pieces of gravel. The fine sand grains or mud tend to hold more water, thus meeting another requirement of this species. Where the water is extremely swift and the substrate is composed exclusively of large boulders, the only member of the genus likely to be found is *H. nudus*.

Associated with the habitat of this genus is the growth of various phyla of microscopic algae upon the rocks. Such a micro-turf may consist of diatoms, desmids, very young growths of the green algae, some of the finer species of the brown algae, etc. Such a turf is essential, being the chief food of members of this genus. Like *Pachygrapsus* species, crabs of this genus spend a tremendous amount of time gleaning the micro-algae from the rocks by means of their large chelae. At night or when the crabs appear to be undisturbed, they may be seen in large numbers foraging along the tops of rocks. It is interesting to note that the males frequently will be found highest up on the rocks while the females are more timid and remain along the lower sides of the rocks where they can reach a hiding place in case of an emergency. As the tide comes in and covers the zone, these crabs move about in large numbers, yet become quite secretive if the presence of the collector is obvious. The behavior of the males as compared with the females was especially noteworthy in *H. nudus.* When females of this species were captured upon the rocks at night they quickly autotomized appendages in order to escape. Males, on the other hand, were quite reluctant to autotomize an appendage but rather would resort to bluffing or actual pinching with the chelae.

*Hemigrapsus nudus*

FOOD AND FEEDING HABITS: Thirty-four specimens were collected in the Titlow Beach area for stomach analysis. The animals were preserved with a 5% formalin solution to insure a quick and complete saturation of the stomach contents. In the laboratory the stomachs were removed and the contents examined under dissecting and compound microscopes. Of the 34 animals examined, 4 had completely empty stomachs while 3 had only partially full stomachs. The largest portion of the gut contents was made up of marine algae, while the second largest portion consisted of inorganic material such as sand grains. The least abundant material found in the gut content consisted of animal tissue. Amongst the algae, diatoms and desmids made up the greatest portion of material. Some species of green algae (*Ulva* sp. and *Enteromorpha* sp.) were frequently found. To determine the source of the diatoms and desmids, scrapings were made along the sides and tops of rocks within the habitat of this species. A microscopic analysis of these scrapings demonstrated that the algae present were identical with those found in stomachs of *H. nudus.* Furthermore, diatoms taken in sea water samples did not match those found in the stomachs. Examination of the rocks showed that young fronds of the above-named green algae were frequently present. Our observations have shown that this species gleans from the surface of the rock using the large chelae. The feeding method is primarily the same as that described by Hiatt (1948:178) for *Pachygrapsus crassipes.* Crustacean exoskeletons made up the most notable portion of the distinguishable animal tissue within the gut contents. Amphipods could be recognized and fragments of other similar arthropods, were present. No attempt was made to determine the exact species of either the animal or plant material, for the source of this material seemed to be the most important thing in this instance. Abundant small arthropods exist wherever *Hemigrapsus* feed and thus these animal fragments are probably accidental in their appearance. Hiatt (1948:178) describes *Pachygrapsus* as being an active predator which will frequently attempt to capture living animals. The present writer has seen *Pachygrapsus* on numerous occasions in California in the act of eating freshly killed animals, even large individuals of newly-molted *Cycloxynthops.* No such observations have been made for *H. nudus* in the field, though there is little doubt that this species will capture and eat animal material when it is available. On occasion this species was seen feeding on dead animal tissue. However, the food supplied by scavenging probably contributes very little to the total volume consumed by this species. Feeding activities are most readily observed at night. When in total darkness crabs will migrate from their hiding places and feed along the sides and tops of rocks. *Hemigrapsus* may confine much of its feeding to periods of low tide to prevent the tiny diatoms from being washed from the chelae, although this species does feed while under water. *H. nudus* is definitely a herbivore, but obtains a small portion of its food as a predator and scavenger.

SYNOPSIS OF REPRODUCTIVE ACTIVITY: Figure 1 shows that oögenesis in *H. nudus* begins in the fall and continues into the first weeks of January. Numerous observations of copulation were made during the later weeks of December and into the first weeks of January. Egg deposition begins very early in January and the rate of deposition increases swiftly until over 70% of the females are ovigerous at the end of that month. The number of females bearing fertilized eggs on the pleopods increases very slowly from this point on, until a peak of 98.6% is reached in the early weeks of April. Hatching very

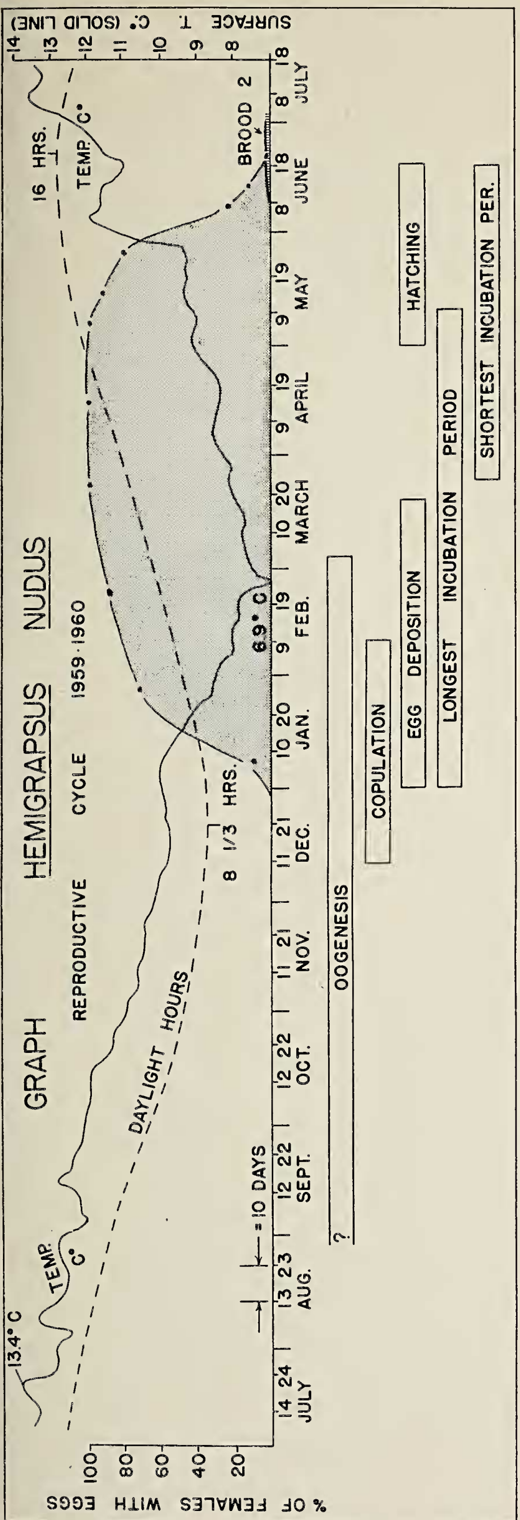



FIG. 1. The reproductive cycle of *Hemigrapsus nudus.*

noticeably begins at about the first week in May and continues, somewhat slowly at first but then increasing in rate, until about the middle of June. Less than 1% of the females examined were found to carry a second brood of eggs. At this time a period of quiescence occurs until oögenesis begins again in the fall. After the middle of July no trace of egg-bearing females could be found at the Titlow Beach collecting site, even though several hundred females were examined at each bimonthly collecting trip.

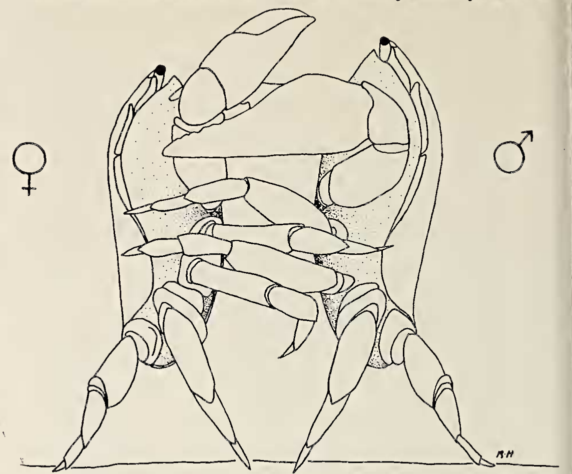
OÖGENESIS: The process of oögenesis probably begins while the female is carrying eggs of the previous brood attached to the pleopods. Of 20 females dissected in the middle of June, 4 showed no visible development (using the technique described above), while the remainder showed some slightly detectable development of ova within the ovaries. In most cases these ovaries were predominantly hyaline or whitish in color, but faint orange or reddish ova could be observed. These, however, were too small to be measured. By the end of September an average measurement of 0.25 mm diameter showed that considerable ova development had occurred. From this point on, development proceeded at a regular but slow pace, and by the end of November ova averaged 0.36 × 0.39 mm in size. From this time on until the time of egg deposition there was only a slight increase in ova size. There was a gradual change in color as the ova developed. In September most of the ova were yellow or yellow-orange in color. The orange color prevailed until November but then showed a gradual change to a deep brown prior to egg deposition.

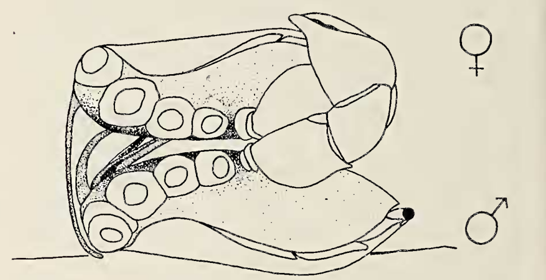
SEASON OF COPULATION: Many records of copulation were made at the Point Defiance laboratory from December 18 to the end of the month. Copulation occurred both during lighted periods and at night. Field records, which are few, suggest that copulation occurs under large stones which afford suitable room and ample protection. Only one period of copulation is necessary as this species, unlike *H. oregonensis*, is single-brooded.

COURTSHIP AND COPULATION: The process of courtship or copulation has not been described for the genus *Hemigrapsus*. One complete account is recorded by Hiatt (1948:199) for a near relative, *Pachygrapsus crassipes.* Hiatt's description, the first for the Grapsidae, clearly shows that this species is strikingly different from other members of the Brachyura in its method of copulation, in that the male assumes an inferior position to the female. Our research attempted to learn the time of copulation in the total reproductive cycle of *Hemigrapsus,* and also to determine if the account given by Hiatt applied to *Hemigrapsus* as well. The discovery that both *H. nudus* and *H. oregonensis* are similar to *Pachygrapsus* in this respect suggests that the Grapsidae in general may differ from most other families of Brachyura.

In December, soon after the shortest day of the year, *H. nudus* was seen on numerous occasions in the act of copulation. Hiatt's notation of the extreme speed with which a pair of *Pachygrapsus* will begin copulation applies also to *Hemigrapsus,* as frequently pairs of the latter genus would be found *in copulo* with no observation of the onset of this act.

*H. nudus* does not precede copulation with a period of courtship, as is the case with many Cancroid crabs as cited by Williamson (1903: 101), Hay (1904:405), Churchill (1918:105), Knudsen (1960:7), and in this paper under the genus *Cancer.* A male initiates copulation by approaching the female and grasping her by the chelae or carapace. After a few seconds to a minute of "wrestling" with variable gestures and shifts in position, the male begins to position the female. The first uniform act occurs when the male lifts the female by her chelae and places her in a vertical position with her anterior end upward and the posterior part of the carapace down on the substrate. Simultaneously the male tilts his body upward in a similar manner so that both male and female come to rest upon their last two pairs of walking legs with their ventral thoracic surfaces in contact (Fig. 2). From this position the male rolls over on his dorsal side with the female held firmly above him. The female is held with her dorsal side upward and her ventral thorax in contact with that of the male (Fig. 3). The male uses the chelae to hold the female by the carapace and uses pereiopod pairs two and three, and on occasion four, to maintain his grasp. The act of penetration of the vulvae by the male's pleopods could not be seen due to our vantage point.




FIGS. 2, 3. Copulation postures of *Hemigrapsus nudus.* Fig. 2 (above): The male has grasped the female by her chelae and is positioning her with his pereiopods, prior to rolling backward. Fig. 3 (below): The male has rolled backward, the female abdomen has been opened by that of the male, and the male pleopods have been inserted in the vulvae. (The legs are not shown for the sake of clarity.)

However, by carefully capturing a pair *in copulo* in such a way as to hold the two firmly in the mating position, the relationship of the male and female abdomens was observed. Such observation, together with accounts in the literature (Hiatt, 1948:199; Knudsen, 1960:7), suggests that the following activity occurred. As the male proceeded to roll from a vertical position to its "back," he simultaneously raised his abdomen in such a way as to hook the abdomen of the female. With a posterior thrust of his abdomen the male then forced the female's abdomen down and thus exposed the vulvae. Mechanically, as the male's abdomen is moved backward, the pleopods or intromittent organs are brought into position for penetration and sperm transfer. When interrupted, or when copulation is completed, the female generally scrambles off backwards while the male attempts to right himself.

Hiatt (1948:199) suggests that *Pachygrapsus crassipes* copulates mainly at night, as his total observations were few in relation to the amount of observation time. In our work, however, we have noted that *H. nudus* was seen most often in copulation during the day under lighted conditions (12 records) rather than at night (2 records). Our observation time during the breeding season was, by far, greater in the daytime and thus we have no firm conclusion as to the preferred time, or light condition, for copulation. Probably this species will copulate at any time that the female is receptive and there is no outside disturbance.

FERTILIZATION AND EGG DEPOSITION: Bimonthly counts of up to several hundred females allowed us to trace the onset of egg deposition through two entire seasons. The date at which egg deposition began and the rate of deposition during the second year was remarkably close to that of the first year for both species, and differed only by about 5 days in either direction. Thus, on or shortly before New Year's Day, egg deposition begins and continues extremely rapidly. Ricketts and Calvin (1952: 31) note that this species produces eggs as early as November in Monterey Bay, California, in contrast to Puget Sound specimens. Perhaps water temperature may have some influence, although in both areas temperatures are declining at the time of deposition. Fertilization occurs as the eggs are discharged through the vulvae, at which time they are attached to the pleopods. A remarkable 98.66% of all females examined were found to have eggs early in April. Nonovigerous specimens examined at this time showed no development within the ovary and probably were unhealthy or beyond a reproductive age. Figure 1 shows that hatching begins rapidly early in May and reaches a peak toward the end of that month. By the first weeks in June all of the eggs have hatched. At this time less than 1% of all of the females examined showed the production of a second brood or a new brood.

PRODUCTIVITY: Fifty-one females of all size classes of *H. nudus* were selected for egg counts. The sizes ranged from 11.9 mm in carapace width up to 34.0 mm in carapace width, and the number of eggs varied from 441 up to 36,456 eggs for the two extremes of sizes. The average number for all 51 specimens was 13,000 per brood. Since only one brood is produced per year this figure probably can be used as the average annual production for this species.

LARVAL DEVELOPMENT: *H. nudus* has been studied and completely described in its larval development by Hart (1935:424–430). There are five zoea stages and one megalops stage.

*Hemigrapsus oregonensis*

FOOD AND FEEDING HABITS: Throughout the year 12 specimens were preserved for stomach content studies. Of the 12, 2 had totally empty stomachs and 2 had only partially full stomachs. Like *H. nudus,* members of this species had been feeding upon diatoms and other algal forms obtained by scraping the upper surfaces of rocks within the intertidal zone. The diatoms were the same sessile forms as described for *H. nudus.* However, most of the individuals had some green algae, probably *Ulva* and *Enteromorpha,* but none had any fragments of animal tissue within the stomach. *H. oregonensis* lives somewhat lower in the intertidal zone than does *H. nudus,* and at this level a large quantity of *Ulva* is found attached to the rocks. Thus, it seems quite natural that this green alga should be used as a source of food. In the laboratory *H. oregonensis* will consume animal tissue such as fish or cut clam or even fragments of crab muscle tissue, and thus must be considered a scavenger when dead animal tissue is available. This species is predominantly a herbivore, however, and is considered to obtain most of its food from plant sources. *Hemigrapsus oregonensis* feeds in the same manner as *H. nudus,* but is more timid in its behavior.

Both *H. oregonensis* and *H. nudus* use the tactile, visual, and chemical senses in their feeding. While gleaning from the rocks at night the tactile senses are presumably used almost exclusively, for the eyes would be of little value in this situation. Chemoreceptors on the tips of the walking legs could possibly be used to determine the presence of marine algae. In the experimental aquarium these species can locate bits of meat by means of chemoreceptors and thus are motivated in their feeding in a manner like that described by Hiatt for *Pachygrapsus crassipes*.

On March 1, 1960, the water temperature in the tanks at the Point Defiance laboratories reached the seasonal low of 6.9 C. This low temperature was maintained for several days running and during this period almost all of the food offered to all species of crabs, including *Hemigrapsus nudus* and *oregonensis*, all three species of *Cancer*, and two species of *Pugettia*, was ignored. Probably this temperature marks a point at which the crab metabolism is retarded and little feeding is required or is possible.

SYNOPSIS OF REPRODUCTIVE ACTIVITY: Figure 4 shows that oögenesis within the ovaries begins sometime during the month of October and continues until the time of ovulation, fertilization, and egg deposition. Egg deposition begins about the middle of February and at about March 10 starts to increase rapidly. Egg deposition is completed at the end of April. In the early weeks of May hatching begins and continues until the end of July. The second brood appears very shortly after the hatching of the first brood begins, showing that there is a very short duration when the females are without eggs on the pleopods. Those females producing a second brood complete egg deposition by the first week of August and hatching is completed by September 24. At this time there is no sign of activity within the ovaries of the female and it is assumed that a period of quiescence is resumed until oögenesis commences once again.

OÖGENESIS: Each month 10 to 12 females of this species were dissected and the ovaries were studied for signs of oögenesis. During October only one individual showed enough development that the ova could be measured (approximately 0.23 mm). In November the specimens showed considerable size increment in that most of the ova were recognizable and measured slightly under 0.20 mm, though 2 of 14 individuals showed ova slightly larger than 0.20 mm. In January the ova averaged about 0.35 × 0.29 mm. One individual out of 8 in this group showed ova only slightly larger than 0.20 mm diameter. The February sample again showed a considerable increase in over-all size, with ova as large as 0.47 × 0.42 mm, but

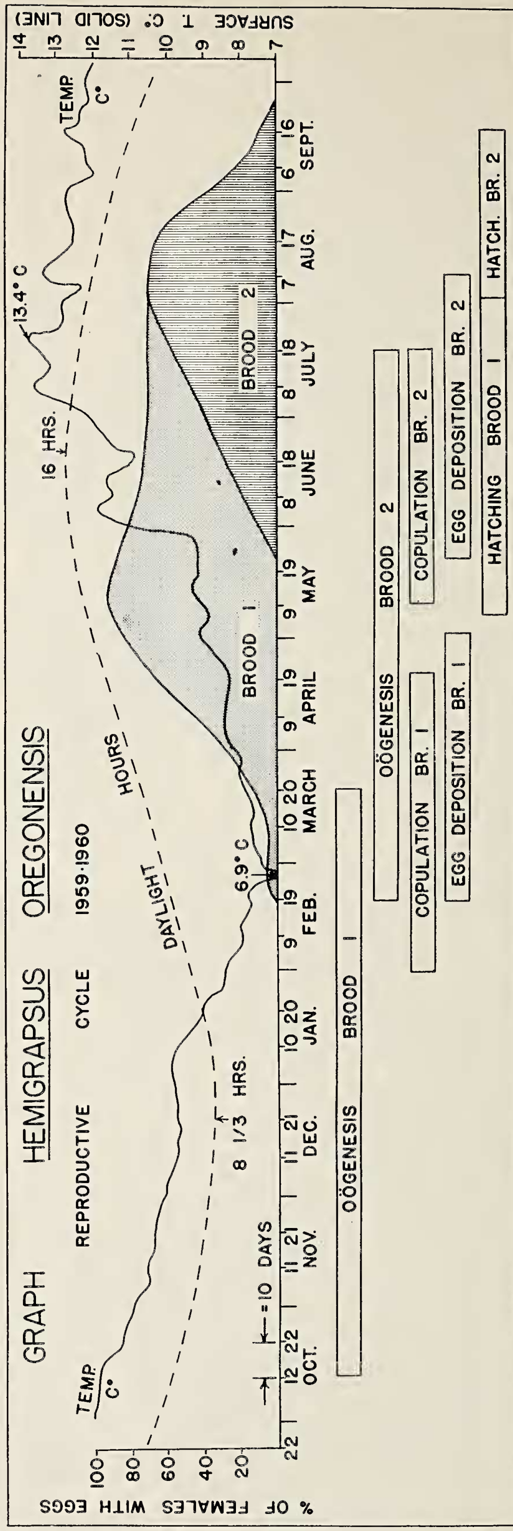



FIG. 4. The reproductive cycle of *Hemigrapsus oregonensis*.

averaging closer to about 0.40 × 0.38 mm. In 10 specimens sacrificed in February, 3 had ova about 0.20 mm in diameter.

The ova begin to take on pigmentation as development occurs. During October most of the ovaries were hyaline, while the one individual showing some development had ova of a rusty brown color. Generally the transition in color is from a light yellow to an orange, to a purplish-brown, and finally to a very dark purplish or orange-brown color.

Oögenesis occurs a second time during the reproductive season in about 70% of the females. The progression of ova development is simultaneous with the embryonic development of those zygotes attached to the pleopods. Very shortly after the hatching of the first brood has occurred, copulation probably takes place and a second brood is brought forth. Inasmuch as histological sections were not made of the ovaries, it was impossible to detect accurately the exact time of the onset of oögenesis. By our technique it would appear that early October is the time when activity can first be recognized with any certainty.

PERIODS OF COPULATION: Very few observations of copulation were made for this species either in the laboratory or in the field. Perhaps the small size of the individual and its drab coloration would account for this in part. Those records obtained were gotten around March 20 and April 15. Using *H. nudus* and its total reproductive cycle as a partial guide, it is suggested that copulation in *H. oregonensis* may begin as early as the first of February and probably continues until about April 20. In any event, it would seem that copulation occurs just shortly before egg deposition. Whether or not a second period of copulation is required is not known. Dissections of the spermatheca of those animals bearing ova have not been completed. Thus, knowledge of whether or not sufficient sperm is stored is lacking. Probably a second period of copulation is required, as in the case of *Pachygrapsus crassipes* (Hiatt, 1948:200).

ACT OF COPULATION: The act of copulation of *H. oregonensis* is similar to that of *H. nudus* and *P. crassipes* although this species, being smaller, may need even less time. The position is typical of that of *H. nudus,* as the male rolls over on his back and positions the female with her ventral thoracic surface against his. The chelae of the male are folded over the carapace of the female, extending in a posterior-median direction, thus forming a V. The walking legs are also used to hold the female or to alter her position. Our observations show that the male generally lifts the female and rolls over, simultaneously positioning her after he is resting on his carapace. Thus, a minor difference between this species and *H. nudus* may exist in that the latter often positions the female before rolling backwards. A somewhat imperfect view of the act showed that the male *H. oregonensis* lowers the abdomen of the female in the manner described for *H. nudus.*

An interesting observation made in an experimental tank may shed some light on the initiation of copulation and thus is given almost in full as it appears in our laboratory notes. A pair was found in copulation and records were taken of the activity. For 25 min the pair remained in copulation with only slight abdominal movements and an occasional leg movement observed. At the end of this period, the female broke away and rushed across the tank where a second male abruptly caught her, rolled over and began copulation. The first male broke up this pair by shaking the new male loose. At this time the female darted under a rock. The male in pursuit, unable to reach her with his thick chelae, backed under the rock and pulled the female out by means of his last walking legs. The male then held the female without copulating, for over 40 min, attempting to position her from time to time. At the end of the period the male successfully copulated with the female until she again broke away. A new male caught the female and, in a fluid movement, rolled over and began copulation. The original male returned and succeeded in freeing the female in order to copulate with her again before she finally escaped to the safety of a rock crevice.

It is of interest, first of all, that at least three of the five males in the aquarium were ready to copulate with the female whenever she was free, while one was even successful in dislodging other males in order to copulate. Second, there were nine other females of this species in the same tank, most of which later produced a batch of eggs, thus proving maturity and fertility.

Moreover, this activity occurred in the middle of the copulatory season when one would expect mating to occur. Thus it would seem that, like many mammals and other well-known animals, the males of this species of crab (if no others) become physiologically ready to copulate early in the season but are not aggressive until the female is ready. Such readiness is probably signaled to the male by some hormone which is released into the water as the last act of readiness prior to copulation. Thus, it is suggested that a hormone or some such chemical stimulus is secreted by the female which excites the male into action. This would answer the question of why the "eager" males did not simply grasp other females which were ever-present in the aquarium. Such a signal or trigger for copulation is not the same as that which begins oögenesis or spermatogenesis, but would only affect a male which had completed the maturation process.

EGG DEPOSITION AND FERTILIZATION PERIOD: As with other crabs, fertilization occurs in this species at the time of ovulation and egg deposition. As the eggs pass down the oviducts, they become fertilized in the region of the spermatheca and then pass through the vulvae and are caught within the "egg basket." The abdomen and the exopodites of the pleopods form the baskets and hold the eggs until they are firmly attached to the endopodites of the pleopods. Bimonthly counts of up to 300 females of this species were made to determine the pattern of egg deposition and hatching. A few individuals begin egg deposition as early as February 18, but the percent of individuals (4.66–5.83) remains very low until about March 10. At this time (see Fig. 4) there is an abrupt increase in the rate of egg deposition for all individuals. Egg deposition continues until about the first week in May, when over 90% of the individuals have eggs attached to the pleopods. According to Figure 4 it would appear that hatching begins very shortly after this peak is reached, for a gradual fall-off in the percent of individuals with eggs is noticed. It is quite possible that those individuals which produced eggs early in February may have begun the hatching process even prior to the peak of egg deposition. This may account for the fact that only 90% of the females are seen with eggs at any one time. When these data are compared with *H. nudus,* it will be seen that nearly 99% of the females may have eggs at one given time. As early as May 20 the second brood of eggs begins to appear for some individuals. Figure 4 shows a sharp increase in the number of females with new eggs, suggesting that only a short lag between broods occurs. A careful check of the condition of the developing embryos continues to show an increasingly large number of new eggs and a correspondingly smaller number of prehatch specimens. A climax of hatching for brood number one is reached shortly before the peak of egg deposition for brood number two, which is around August 6. The percentage of females producing two broods drops to about 70% and shortly after the peak is reached hatching again occurs and continues until September 24, when less than 1% of the individuals still have eggs in the prehatch condition.

To demonstrate more fully that a second brood is produced 38 females were dissected on June 13, shortly after brood number two had begun to appear. Of the 38, 22 had no eggs attached to the pleopods, while 16 had new eggs attached to the pleopods. Of the 22 specimens without eggs all but 6 had well-developed ovaries that were visible through the membranous wall of the abdomen and upon dissection showed fully developed ova. Five of these 6 showed little or no development of ova within the ovaries while the sixth specimen proved to be immature and thus not ready for reproduction. Of the 16 individuals bearing new eggs none had well-developed ova in the ovaries, showing that these had now been spent on a second brood. Three of this latter group showed some very slight development in the ovaries in the way of pigmented eggs. It is suggested that these eggs simply were not ovulated at the time of deposition and hence remained to give the appearance of slight development.

On May 15 the number of females bearing their first brood of eggs reached 59% of all of the females observed. A special measurement of the 326 females collected was made to determine the relationship between size classes of those females with and without eggs. Gradations of 2 mm from 8 mm to 20 mm were used so that crabs closely approaching one gradation or another were simply grouped into that size class. Figure 5 shows the distribution of those females with and without eggs. It will be noted that the 12 and 13 mm size range contained the largest number of reproductive and nonreproductive females, and that the total number of individuals drastically drops off on either end of the curve. It will be noted that the two curves are amazingly similar, indicating that egg deposition does not necessarily occur earlier in larger or smaller size classes, but that the period of deposition is irrespective of size class and is determined solely by the season itself.

PRODUCTIVITY: Egg counts were made for 42 specimens of *H. oregonensis.* The number of eggs ranged from around 800 to over 11,000 per brood. The average for the 42 specimens was 4,500 eggs per brood. When the number of eggs is plotted against the width of the carapace, it can be seen that the number of eggs increases in almost a straight line until a size class of 12.5 mm is reached. At this time the line breaks, indicating that the number of eggs produced actually increases above the expected rate of production for the smaller animals, as the carapace size increases. As many as 22,000 eggs could be produced in a single year by some of the largest females which produce two broods. For those females that have two broods a year the average production would be about 9,000. However, since only about 70% actually produce the second brood, on the basis of 100

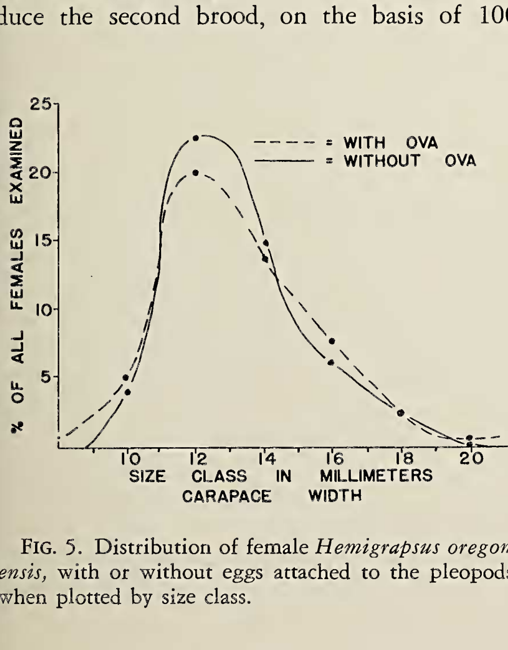



FIG. 5. Distribution of female *Hemigrapsus oregonensis,* with or without eggs attached to the pleopods, when plotted by size class.

individuals a yearly average of 7,650 would be obtained. This latter figure is probably more accurate for the population as a whole and is used to denote annual production.

LARVAL DEVELOPMENT: The larval development of this species has been worked out by Hart (1935:430–432), using specimens taken from Vancouver Island, British Columbia, which is close to the latitude of our own studies. She lists the time required for development to the first crab stage in two individuals as being 4 and 5 weeks. If the southern Puget Sound specimens develop at a similar rate, the first crab stages could reach the beach in the early weeks of June and continue to arrive into October. Hart has completely illustrated the larval stages of *H. nudus* and has given sufficient data on *H. oregonensis,* so that those extremely similar larvae may be separated when taken in plankton.

## POSSIBLE TRIGGER MECHANISMS

In a study of trigger mechanisms which may initiate the reproductive processes, several possibilities must be considered: is the reproductive life cycle triggered at its very beginning, in the species being studied, and then do all subsequent events simply follow suit as in a chain reaction? Or does each individual event such as oögenesis, copulation, egg deposition, etc., have its own individual triggering device? A review of the literature has shown that most generally photo-period, temperature, or a combination of both serve as triggering mechanisms for reproductive activity amongst the invertebrates and many of the vertebrates. Since a parallel, though sometimes lagging, physiological cycle progresses almost concurrently with the annual cycle of external stimuli, a study of trigger mechanisms must eventually include a careful study of hormone and other physiological activities. Although many experiments were attempted in our research, none produced results of sufficient magnitude to warrant in this paper a review of the literature concerning trigger mechanisms, or an exhaustive description of experimentation. Experiments were set up during several parts of the year where temperature and photo-period were either increased, decreased, or maintained at a steady state, either simultaneously or independently, and the species of *Hemigrapsus, Lophopanopeus,* and *Petrolisthes* were subjected to these artificial environmental changes. In comparing the life histories of *Hemigrapsus oregonensis* and *H. nudus* several events notably occur just after significant changes in photo-period or temperature have occurred. Namely, in *H. nudus* (Fig. 1) copulation begins at about the shortest day in the year and progresses steadily as the photo-period lengthens. However, in this cycle there is no correlation with temperature, as the temperature has slowly been decreasing prior to the onset of copulation and after the period of copulation. At the end of this reproductive cycle the temperature is still somewhat on the rise, but the photo-period has again reached its peak and the days begin a shortening trend at the time when the last of the larvae hatch. It is conjecture to do more than suggest that there may be some correlation between the life cycle and this trend from the shortest photo-period to the longest photo-period. On the other hand, the life cycle of *H. oregonensis* (Fig. 4) seems to parallel the trend of temperature with reference to egg deposition and the maintenance of the first and second broods. That is, egg deposition of the first brood begins rapidly after temperatures start to rise in March, and the second brood does not complete hatching until temperature has reached its peak and has begun a downward trend. The exact time at which copulation is most prevalent for this latter species is not well known and hence this event cannot be paralleled with photo-period or temperature. In both species the seeming correlation between environmental factors and reproductive activity failed to account for the onset of spermatogenesis or oögenesis. It is quite possible that the original triggering stimulus was received during the summer or fall prior to oögenesis and spermatogenesis, and that subsequent reproductive behavior simply followed as a chain reaction probably triggered by hormone activity. That hormones are important is clearly seen in the data given for *H. oregonensis,* where it is noted that some probable chemical stimulus caused males to mate only with certain females and to ignore all others. The striking difference between the two species of *Hemigrapsus* suggests, however, that different external stimuli may be influencing the onset of reproduction in these two species. Because of original mistiming of experimentation, which was based on reproductive activity as recorded in the literature, and a series of mechanical difficulties in cooling and lighting devices, our data are incomplete and inconclusive in this aspect of research. Thus, we will reserve this problem for later research and publication.

## FAMILY XANTHIDAE

### *Lophopanopeus bellus bellus*

HABITAT: The pebble crab, *Lophopanopeus bellus bellus,* is replaced in the south by its counterpart, *L. bellus diegensis.* As shown by Knudsen (1960:171) this species differs from the *Lophopanopeus* complex of *leucomanus* in that it prefers the more quiet water of bays or estuaries to the open ocean shores. The writer finds *L. b. bellus* occupying a micro-habitat identical to that of *L. b. diegensis* in the south. The former subspecies is found in Puget Sound at the lower extremes of the intertidal zone and seems to prefer a situation where a single layer of rock covers fine sand or mud. Rocks which do not fit closely to the substrate, but leave a slight gap underneath, are less frequently occupied by this crab. On the other hand, this species burrows well back under large rocks that hold so firmly to the substrate that hydrogen-sulfide mud is produced. Like the southern subspecies, the Puget Sound form often "plays dead" for a few minutes when disturbed in its hiding place. Way (1917:367) states that this crab is always found with *Cancer oregonensis* buried in sand and mud under rocks on rocky shores. Around Titlow Beach and Point Defiance the two species often occur together but *Cancer oregonensis* is also found higher up in the intertidal zone. Our collecting records indicate that not all rocky shores are suitable for *Lophopanopeus.* In all cases where this crab is found there is a noticeable water current, though often not strong, during the ebb and flow of the tide. The presence of a tidal current is the only factor that the present writer finds to separate the *Lophopanopeus* habitat from almost identical, adjacent stretches of beach where *Lophopanopeus* is not present.

FEEDING HABITS: Stomach analyses were made for seven individuals. The nature of the material in the stomachs made identification of the fragments quite difficult, as compared with fragments obtained from herbivorous species such as *Hemigrapsus.* Within the various stomachs were found fragments of brown algae (sp. ?) and some form of green plant which resembled *Zostera.* Diatoms similar to those found in the stomachs of *Hemigrapsus* were also present in a few of the specimens. A peculiar whitish material, more or less well broken up, and resembling coralline algae was also found. As recorded by Knudsen (1959:114) this genus feeds to a large extent on coralline algae of the species *Corallina gracilis, C. vancouverensis, Bossia orbigniana,* and *B. gardneri.* Encrusting and free-living coralline algae are found in limited quantities in the Puget Sound habitat of *Lophopanopeus* and thus may be used as a food source by this species. Some animal tissue (crustacean, mussel, and barnacle fragments, and nematode worms) was also found. The nematode worms are believed to be stomach parasites, however, and not a food source.

SYNOPSIS OF REPRODUCTIVE ACTIVITY: Figure 6 shows that oögenesis begins in the autumn and continues until the time of egg deposition. The ova reach a near maximum size in December and then increase in size very slowly until the time of deposition. Fertilization and deposition begin in the early weeks of January and continue very rapidly throughout the month of February. Early in March a leveling-out is reached, with a high of 92.3% of the females bearing eggs. Our observations and those of Hart (1935:414) show that hatching begins in May but the appearance of brood number two tends to offset hatching as far as the percentage of females bearing eggs is concerned. Thus, Figure 6 shows a slow increase until the first week of June, at which time the hatching of brood number one sharply increases and offsets the rising curve of brood number two. About 60–70% of the females produce a second brood which matures rapidly and hatches, probably, throughout the month of September. A solid line on Figure 6 indicates that accurate field measurements have been made to substantiate the curve, but a broken line indicates that field data are few, or lacking. A brief period of quiescence follows the second brood and then oögenesis begins again in the fall.

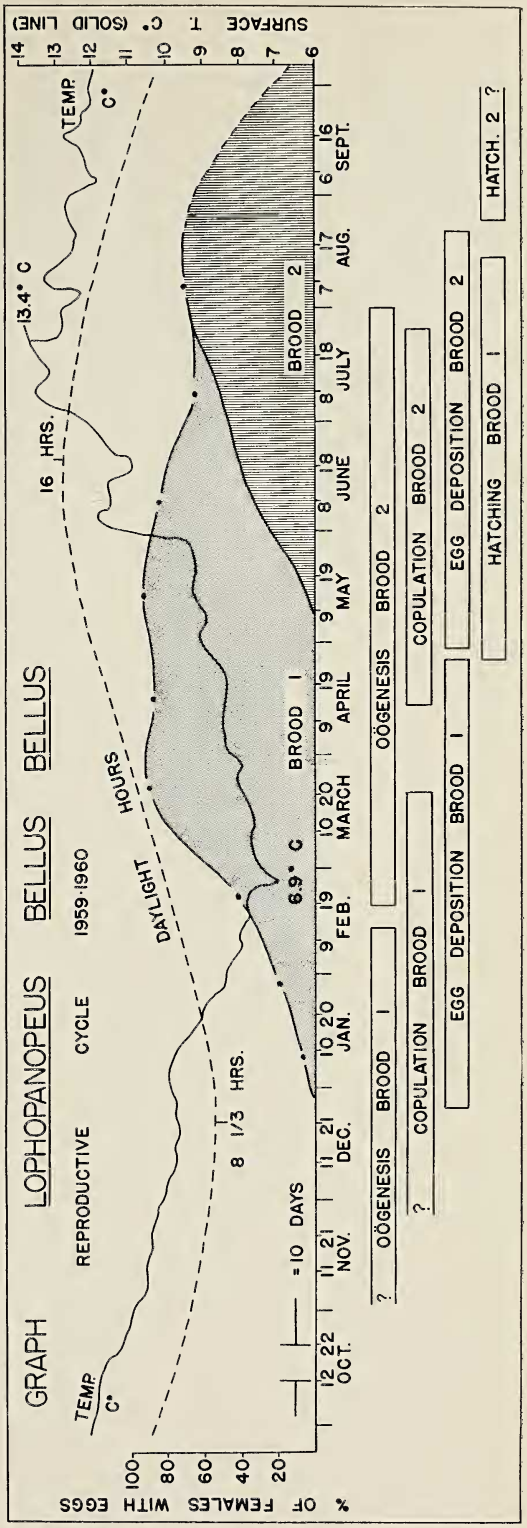



FIG. 6. The reproductive cycle of *Lophopanopeus bellus bellus.*

COPULATION: Many records of copulation in *L. bellus bellus* were obtained in the laboratory but none were obtained in the field. The season of copulation is just prior to egg deposition. This would suggest that only a brief period of a few days or weeks separates copulation and egg deposition. On June 9, seven females were dissected which had just hatched their first brood. Six showed ovaries in a highly developed and ovigerous condition, while one had ovaries showing no development. Of the seven, four had the spermatheca completely empty while two had a small amount of sperm present, and one had a large quantity of sperm. These data suggest that copulation is necessary prior to the second brood. The process of copulation in this subspecies is identical with that of *L. bellus diegensis* as described by Knudsen (1960:7).

PRODUCTIVITY: The eggs in egg masses taken from 20 females of various size classes were counted and the average was determined. The number of eggs per brood ranged from 36,000 down to 6,000, with an average for the 20 animals of 15,640. Thus, an average for all females having two broods in a year could be 31,000 eggs per year, but with only about 90% of the females producing a first brood and only about 70% producing a second brood, a more accurate average for all females with or without eggs would be about 25,000 eggs per year. The average egg count given here is extremely high as compared with *L. leucomanus leucomanus* (Knudsen, 1960:9) but the size range of the northern *L. b. bellus* is much larger than in those specimens counted for *L. l. leucomanus.*

LARVAL DEVELOPMENT: The larval development of *L. bellus* was studied and fully illustrated and described by Hart (1935: 414–420). Since that time Menzies (1946:1–45) made a revision of the genus *Lophopanopeus* and has placed *L. diegensis* Rathbun in the *L. bellus* complex, making *bellus* and *diegensis* subspecies of the species *bellus.* After Menzies' revision, the larval development of *L. bellus diegensis* was described by Knudsen (1959:57–64) and the larval development of *L. leucomanus leucomanus* was also studied (Knudsen, 1958:51–59).

POSSIBLE TRIGGER MECHANISMS: The early part of the visible life cycle of this species is similar to that of *Hemigrapsus nudus* in that copulation occurs during and after the shortest days of the year and egg deposition begins about the same time as in *H. nudus* and continues as the photo-period lengthens. When daylight has reached its maximum length in June the second brood (which is lacking in *H. nudus*) begins and continues to follow the rise in water temperature. While there seems to be some correlation between photo-period, temperature, and the timing of brood number one and brood number two, data to support such correlations are lacking.

## FAMILY CANCRIDAE

*Cancer oregonensis*

HABITAT: Of the Puget Sound cancroid crabs, *Cancer oregonensis* is somewhat unique in that not all of the individuals migrate during the reproductive season, but rather many remain in a consistent area within the overall habitat. This species is consistently found with *Lophopanopeus bellus bellus* and slightly above the latter species within the intertidal zone. The habitat requirements seem to be almost identical with those of *Lophopanopeus.* It is also common to find this species high up on pilings which are heavily encrusted with barnacles and mussels. In this situation *C. oregonensis* selects a small cavity between the encrusting organisms and uses this for its home site. It feeds on barnacles and other marine organisms within and around this home site.

FEEDING HABITS: While a large number of *C. oregonensis* stomachs were dissected during the routine of counting eggs and measuring ovary development, only a few animals had food within the stomachs. The rest, apparently, were not feeding during periods of reproductive activity. Prasad and Tampi (1951:675) report that females of the cancroid crab *Neptunus pelagicus* do not eat while carrying eggs on the pleopods, as is suggested here. The gut contents of eight individuals, five females and three males, were analyzed. In some, partially digested material resembling polychaete worms with numerous bristles was found. In others, fragments of crustacea such as amphypods, small shrimp, or crabs were found. One animal had the stomach completely filled with red eggs identical to those carried on her own pleopods. There is little doubt but that this crab had been eating its own eggs. Whether these were fertile or not is difficult to say as the eggs were extremely new. One male specimen contained algae fragments which resembled *Ulva.* While this species is all but impossible to observe in the field, many observations of feeding and other activities have been made in the Point Defiance aquarium. Whenever barnacles are available this crab will feed almost exclusively on them, to the extent that it will ignore fresh-cut fish placed in the aquarium. In the public display rooms this crab often becomes a nuisance by continuously crushing barnacles and littering up the tanks with fragments of barnacle shells.

REPRODUCTIVE ACTIVITY: Courtship and copulation in this species is concurrent with the molting process of the female. The months of April, May, and June mark the peak of female molting and probably of copulation. On April 14, 43 females were located at the Tacoma Narrows and many of these were in the process of courting or copulation. Again upon June 8, 11 females of 69 encountered were in the process of courting. Six of the 11 females showed that the epimeral line was broken, indicating that ecdysis was soon to occur. In August, 10 females were collected at random and dissected to determine if sperm was in the spermatheca. Of the 10, 4 had full spermatheca, 2 had some sperm, and 4 had empty spermatheca. These few data suggest that copulation may occur any time during the late spring or summer, and that sperm is stored until the time of egg deposition in the late fall. Ovaries that were studied in May showed no evidence of oögenesis, though some were milky white in color. Dissections made in June showed 3 out of 5 specimens with ovaries whitish to clear, 1 with the ovary whitish in color and showing some development of the follicles, and 1 showing large yellow follicles. Of the 10 specimens dissected in August, 3 showed considerable development of the ovaries, while 7 were underdeveloped. All specimens with developed ovaries had some sperm in the spermatheca, but not all animals with stored sperm showed ovary development.

Fewer females were found in the field during the time of egg deposition and incubation than at other times in the year. Females with eggs were encountered during the last weeks of November. All females collected through the middle of February had eggs attached to the pleopods. However, the numbers of individuals of this species encountered were so small (the highest being 18 females with eggs out of 18 encountered on January 26) that no graph will be presented. In April and in June an occasional female with eggs was encountered. These latter records were considered to be second-brood individuals.

In conclusion, it would seem that oögenesis occurs in the summer and fall, that egg deposition begins in the last weeks of November, that eggs are carried until the middle of February when hatching is completed, and that hatching is followed by a period of quiescence, molting, and finally copulation, in that order.

COPULATION: Our field observations of *Cancer oregonensis* show that this species tends to court as other cancroid crabs do, and that the male carries the female about for several days prior to molting, then copulates with the female after she has completed the molting process. The male will continue to court or protect the female until her shell is hard enough for her to resume normal activity. This species may be more secretive than the larger species, *Cancer productus,* and hence observations of courting pairs moving freely about under water were not made. During periods of low tide, however, numerous courting pairs were found buried deep under rocks in little pockets surrounded by fine grained sand. The male assumes the normal superior position over the female and remains hidden during the courtship period. By carefully grasping the courting pair, it was possible to see the male with the pleopods inserted in the vulvae of the female. The very secretive behavior of courting and copulating pairs, in contrast to *C. productus,* suggests that this species is unique in its courtship. Courting pairs found in barnacle masses high up on pilings remain well hidden between barnacles during courtship. In the laboratory courting pairs had less chance to hide themselves, but nevertheless burrowed down into the gravel substrate and remained as concealed as possible.

PRODUCTIVITY: The eggs within the egg masses of 17 *C. oregonensis* females were counted to determine their seasonal productivity. Sizes of the females varied from a carapace width of 17 mm to 26 mm, and the number of eggs ranged from 10,000 to 33,000. For 17 individuals counted, the average productivity per brood was 20,540 eggs per female. Usually there is only one brood per year and those females producing a second brood or, perhaps more correctly, a late brood, are rare. Thus, the average of 20,540 represents the seasonal productivity for this species.

*Cancer productus*

HABITAT: Geographically, *C. productus* is found from Alaska to Magdalena Bay, Baja California, in two major types of habitats. Primarily it is found in bays and estuaries, such as Puget Sound, Grays Harbor, Willapa Bay, and other similar areas in the state of Washington and up and down the coast. The second type of habitat is that classified as a "protected rocky coast," which could be characterized by any of the small rocky bays or inlets along the open ocean front where rocky headlands or other rocky obstructions cause wave refraction and thus create a zone of less violent action. This second type of habitat is perhaps a minor one. *C. productus* is found under these conditions at the Tacoma Narrows in Puget Sound.

The writer considers the primary habitat of this species to be that of the large bay or sound. Schmitt (1921:222) notes that *C. productus* is remarkably absent from fine sand and mud substrates in San Francisco Bay. Rather, he lists this species as being found largely upon sand, gravel, or rock substrates. Cleaver (1949:70) mentions that *C. magister* remains generally in areas with sand or mud bottoms in the bays along the Washington coast. He states that while this species may occasionally be found on rock or gravel, it is, as a rule, replaced by *C. productus,* which is predominant in such situations. Weymouth (1914:124) suggests that *C. productus* lacks a straining apparatus to prevent fine particles of mud and sand from entering the gill chamber. Thus, this species is restricted to those zones which will allow it to bury itself in the substrate without clogging the gill chambers. Our own observations in Puget Sound coincide with those of Schmitt and other workers, for this species is frequently found around the Point Defiance boathouse, under the dock at Titlow Beach, and in many similar areas in which the substrate consists of hard packed sand, gravel, or broken shell fragments.

Our observations suggest that this species is equally active at night or in the daytime. Due to its large size *C. productus* has few enemies within the zone of its normal activity. While many of the very large rock fishes, octopi, or other marine animals will prey upon this species, and other crabs as well, these predators are normally absent in the most favored microhabitat of *C. productus.* When inactive this species may be found hiding at the base of pilings, where it buries itself beneath gravel or shell fragments, or else hides beneath sunken logs or rocks which loosely cover the substrate. Extremely rarely does one find this species hiding in hydrogen-sulfide mud.

The time and place of activity or inactivity of *C. productus* seems to be governed mainly by the "choice" of the individual, its age or sex, or the particular phase of reproductive activity or molting activity carried on. A survey of our bimonthly reports for 2 years of collecting shows that from January through May males are predominant in the intertidal zone, while females are almost totally lacking. Those few females encountered during this time were, with one exception, without eggs. From the end of May on into June the sexes are almost equally distributed in numbers, while the females predominate throughout the summer months up into early October. Then the males and females are almost proportional in numbers throughout November and December. Males were never totally wanting in our field collecting at any time of the year, as were female specimens. As will be noted under *Reproduction,* presence or absence coincides well with the period of egg development, molting of the males, and the times of copulation. Juvenile specimens were abundant only in areas adjacent to those occupied by the adult individuals. These observations suggest that males and females may have a horizontal migration to the deeper water during periods of the year, or they may become inactive and extremely secretive and thus remain carefully hidden within the habitat area. Cleaver (1949:70) reports for *C. magister* that:

An interesting feature of this species is the tendency to aggregate by size and sex. Until a width of two or three inches is reached, crabs of both sexes are found together in approximately equal numbers. With the onset of sexual maturity, a definite segregation occurs. Adult females are comparatively rare in Grays and Willapa Harbors, although in some areas of the ocean they are overwhelmingly abundant, particularly in the late winter and early spring months.

Cleaver further notes (1949:67) that some data suggest an offshore migration for this species and confirm a coastwise migration. It is quite possible that *C. productus* may be similar to *C. magister* in having an offshore or vertical pattern in migration. Prasad and Tampi (1951: 676) show that other members of the family Cancridae, in particular *Neptunus pelagicus,* segregate according to size and sex in a manner similar to that described above.

It was interesting to note that this species displays a negative rheotaxis in response to the lowering of the tide. It was frequently observed that this species continuously moved ahead of the receding tide, without being "pushed" by the edge of the water or the reduction of the water level. In experimentation, crabs were released into a 3 × 8 ft aquarium and allowed to become tank-adapted. It was noted that they moved about at random in the aquarium. At this time a stream of salt water was introduced at one end of the aquarium, so that a current was created along the bottom of the tank. The crabs oriented themselves and began moving in the direction of the current. The rate of crab movement roughly corresponded to the rate of current created in the tank. It is suggested that this species responds to weak currents created as the water recedes in the intertidal zone, and may govern its tidal migration mainly by these currents.

FOOD AND FEEDING HABITS: *C. productus* is not secretive in its feeding but, rather, is often bold in its attempt to obtain food. It was regularly observed feeding on barnacles attached to pilings, or on dead fishes or other animal matter available in the habitat. Discounting the food supplied by fishermen in the form of cast-away fishes, barnacles seem to be the most consistent source of food. *C. productus* will feed around the base of pilings, or will climb up on the pilings in order to obtain this food. The large chela is used in breaking barnacles, while the smaller chela serves to transfer the barnacle to the mouth parts. Crabs of this species maintained at the Point Defiance aquarium frequently captured and ate smaller crabs of the same species or other species. At such times *C. productus* merely waited motionless until the smaller crabs approached within striking distance, then lunged forward to capture the smaller crab, crushing the carapace with the large chela. In feeding experiments where crabs were secretly fed small pieces of fish with no light available for their vision (they were observed under red light), *C. productus* was able to locate pieces of food in a brief time. If water was circulated through the tanks at the time of feeding, so as to distribute the meat juices more readily, the time required for locating food was greatly decreased. Probably this species uses tactile receptors, chemoreceptors, and eyes, either individually or in combination, in its feeding.

REPRODUCTIVE ACTIVITY: Because of the secretive nature and/or disappearance of females during part of the reproductive season, field data are almost wanting concerning some phases of reproduction in *C. productus.* Many animals were maintained in the laboratory in order to augment our field observations. Copulating pairs could be found at almost any time of the year though they were numerous only in the summer and fall months. Beginning in June and continuing on through July and August mating pairs are encountered regularly and in large numbers. Only one or two pairs were observed as late as the first of November. This species, like the other cancroid crabs, copulated just after the molting of the female. Egg deposition begins for a few individuals as early as October, and individuals may be found carrying eggs on the pleopods as late as the early weeks in June. Our records would tend to indicate that most of the females extrude eggs by December or January, and that most eggs hatch by late March or early April. In the laboratory three females which extruded eggs prior to December 20 had completed the hatching process by March 6. Two of these females then extruded new, but small, clutches of eggs without first molting or copulating. However, it was impossible to maintain these females until the time of hatching, though the eggs appeared viable and in the process of development. Thus, it is not known if the female has sufficient stored sperm to fertilize a second brood, nor whether this is typically carried out by females of this species. Ovaries removed from ovigerous females in March most frequently showed no development, though a few had some eggs apparently left from the previous brood. Cleaver (1949:79–80) states that May and June are the peak months for copulation in *C. magister* and that the majority of the females carry eggs between the first of November and the last of February. A check of this latter species by Cleaver on February 19, 1947, showed that 86.5% of the females had or were carrying eggs. Thus, there is a similarity in the timing and the procedure of the reproductive cycle of *C. magister* and *C. productus*. Both show a considerable lapse of time between copulation and egg deposition. The eggs of *C. productus* are bright orange when first deposited. These gradually become more brownish in color and become hyaline and gray by hatching time. Egg masses were not counted for this species.

COPULATION: Copulation of *C. productus* is similar to that described in this paper for *C. oregonensis* and by others (Churchill, 1918:105; MacKay, 1942:18; Cleaver, 1949:79–80; Knudsen, 1960:7), in that a courtship period precedes the molting of the female and copulation follows the process of molting. As discussed for *Hemigrapsus oregonensis* in this paper, there seems to be some attraction, such as the release of molting-hormones by the female, so that males may identify females that are about to molt. Unlike *Cancer magister* (Cleaver, 1949: 80), pairs of *C. productus* do not separate following the act of copulation; rather, the male continues to protect the female for several days. A check of the female exuvium shows that the spermathecae are removed at the time of molting, as recorded by Cleaver. Unlike *C. oregonensis,* this species does not go into seclusion during the time of courting, but moves freely about at this time. Courting pairs are frequently seen up on pilings where the male may feed, or running across the sandy substrate. In the aquarium captive males tend to be polygamous, as is suggested by Cleaver for *C. magister*.

*Cancer gracilis*

HABITAT: For a discussion of the habitat of *C. gracilis* see *C. productus*. This species was encountered only in sympatry with *C. productus* when the former species was present in the intertidal zone. However, the habitats in which both species occur are quite sandy, and approach the extreme in sandiness for *C. productus*.

FEEDING HABITS: No analysis of stomach content was made for *C. gracilis*. This species was seen feeding in the identical situation with *C. productus*. Crabs were common both on the pilings, feeding on barnacles, and at common mess with *C. productus* feeding on fish detritus. From general appearances it would seem that this crab uses approximately the same food as *C. productus*.

REPRODUCTIVE ACTIVITY: Field records for *C. gracilis,* other than those of copulation and courtship, are almost totally wanting. Our laboratory records suggest that the reproductive cycle is about identical with that of *C. productus*. Females in the laboratory produced egg masses between the months of December and April. Whether or not a second brood is produced in nature is unknown, as only a few laboratory animals produced a second brood. However, the known second broods produced in the laboratory consisted of very few eggs as compared with the normal brood. The time of courtship and copulation coincides with that of *C. productus*.

COPULATION: During the summer months numerous pairs of *C. gracilis* were seen feeding under the pilings at Point Defiance. However, during the reproductive periods of the year pairs or individuals became less abundant and soon became absent from the intertidal fauna of those areas observed. From a few pairs isolated in the Point Defiance aquarium and from some field observations we have noted that the process of copulation and courtship is identical with that of *C. productus*. Courting pairs of *C. gracilis* were found amongst other noncourting individuals and would move about the substrate very freely. The larger size of this species may account for the fact that it needs little protection, as does *C. oregonensis*. Males were discovered carrying both hard-shelled and soft-shelled females. When the female of the pair was soft-shelled, most frequently the pair was in the act of copulation. Unlike *C. magister,* the males of this species protect the females after copulation.

## FAMILY MAJIDAE

MOLTING: It has been suggested by Drach (1939:106–377) that the spider crab *Maia squinado* reaches what is known as a puberty molt, at which time no further molting occurs. At the time of the puberty molt crabs of the Majidae become sexually mature and then begin egg production. This is contrary to the other brachyuran families found in Puget Sound, for which molting continues after maturity.

In order to test Drach's theory for the Puget Sound majids a number of experiments and field observations were attempted. Animals were maintained in the laboratory for up to 9 months without any molting. Such experiments became unsatisfactory in time as feeding and overcrowding became problems in the aquaria. A female *Pugettia producta* was encountered on November 14, just after having completed molting, but the exuvium became lost before it was noted whether or not this was immature or mature. Several additional molts of this species and of other species of Puget Sound spider crabs were recorded, but in all cases these were either prepuberty molts or puberty molts and none demonstrated that molting occurs after the puberty molt. Likewise, no exuvia of mature females were ever located on the beaches, as were those for other families of crabs.

If there is a puberty molt and the female spider crab autotomizes a leg either prior to or following the puberty molt, then regeneration (or at least complete regeneration) would be impossible. With this thesis in mind, a series of experiments and field observations was begun where mature animals with partially regenerated limbs were collected and maintained in the laboratory, and additional specimens were brought into the laboratory and were forced to autotomize limbs. In no case did any of the partially regenerated limbs continue to develop when additional molts were lacking, and no other method of regeneration was used. Freshly autotomized appendages of mature individuals showed the primary stages of regeneration which consist of scabbing, but no papillae or subsequent growth occurred. Thus, one must conclude that adults with partially regenerated limbs completed this regeneration prior to the puberty molt, at which time the growth ceased.

Some inconclusive light was shed on this problem when specimens of *P. producta* were dissected. On one occasion a female which had recently completed hatching a brood of eggs died in the aquarium. This animal was dissected and it was noted that the spermatheca was completely empty but that the ovaries were extremely well developed and laden with "ripe" eggs. This demonstrated that a new reproductive cycle was in the making and suggested that a molt could occur at this time, as would be true for other families of crabs. However, no new integument was formed beneath the exoskeleton as can be seen in crabs about to molt. The old integument, moreover, was firmly attached to the exoskeleton, suggesting that no premolt metabolic activity was occurring. Numerous field dissections gave the same data.

A size differential found in sexually mature females of *P. producta* suggests either that the number of molts prior to the puberty molt is not consistent in all specimens, or that molting may continue after sexual maturity is reached. Another somewhat negative point is found in the encrusting organisms living as commensals on the carapace of *Pugettia.* The majority of the specimens bearing eggs have no encrusting organisms such as barnacles on the carapace, which suggests that these animals have recently molted. Whether or not this molt was the puberty molt is unknown. Some individuals, on the other hand, have barnacles which appear to be far larger than one-year old animals and suggest that they have been growing on the carapace for more than a year. This tends to rule out the fact that these individuals have molted in the recent past. Although all of these data are somewhat negative and could readily be ruled out by one positive datum, they strongly support the theory that spider crabs cease molting following sexual maturity.

### *Pugettia gracilis*

HABITAT: The graceful kelp crab, *Pugettia gracilis,* ranges from the western extremity of the Aleutian Islands eastward and southward to Monterey Bay (Garth, 1958:196–197), and from the intertidal zone down to about 40 fathoms (Way, 1917:371). Way records it as being abundant everywhere in the Friday Harbor region in eel grass (*Zostera marina*), while Hart (1930:106) records it from kelp ribbons at Parry Bay. In the southern Puget Sound region the majority of our specimens are found attached to those pilings which were very heavily encrusted with barnacles and other fouling organisms, or clinging to similarly encrusted rocks under the Narrows Bridge. Less frequently were specimens taken from *Zostera* beds. Those individuals taken from *Zostera* were frequently smaller, immature animals. The requisites for the habitat of this animal seem to be an area where there is, first, abundant food, and second, some situation where the crab may get up off the bottom and thus be exposed to continuous currents. Probably the currents are necessary for the crab's survival. It is interesting to note that Garth (1958:199) lists the specimens from the Hopkins Marine Station at Monterey Bay, California, as not being from the intertidal zone. The fact that this species occurs below the intertidal zone in the south, where temperatures closely approximate those temperatures of the northern intertidal zone, would indicate that temperature may be a southern limiting factor. For at levels below the intertidal zone in the south this species could find a suitable habitat and source of food and still enjoy a much colder range of temperatures. Like *Pugettia producta* this species also has the dactylae somewhat modified for holding on to kelp. This species may be more abundant in kelp than our records indicate, as our collecting in kelp was very limited.

REPRODUCTIVE ACTIVITY: *P. gracilis* was often encountered at the Tacoma Narrows and was occasionally found at Point Defiance, but seldom were more than just a few of these animals seen at any time. Thus, the total number of records for this species is too small to be of great significance. Garth (1958:199) cites collecting ovigerous females at Coos Bay, Oregon, when 14 of 16 specimens were with ova in late June, and in mid-July at Bodega Bay, California, in March and at Stewarts Point in November. In Puget Sound we have collected ovigerous females almost every other month throughout the entire year. During 4 of the 6 months in which no ovigerous females were encountered, only immature specimens were collected, and during 2 months, July and October, mature but nonovigerous specimens were observed. Specimens with very new dark purple eggs, intermediate reddish-brown eggs, or grayish-brown prehatch eggs could be found during almost any month of the year. Hatching was most frequently observed in May and June both in the laboratory and in the field. On the other hand, five out of eight specimens collected during the first week of August had very new dark purple eggs. It is not known whether one or two broods of eggs are produced annually.

PRODUCTIVITY: The eggs within the egg masses of five specimens were counted. The hepatic carapace width of these specimens ranged from 20 mm to 25 mm, and the number of eggs per brood range from 6,200 to 13,300, with the average being 10,500 per brood.

COPULATION: Accounts of copulation in the family Majidae seem to be absent in the literature. The secretive nature of the spider crabs would probably cause such a vital process to go unobserved in the field or laboratory. Probably copulation occurs while the crabs are on pilings and thus the chance for observation may be poor. Detailed observation of *P. gracilis* in copulation was possible on only three occasions.

The remarkable fact seems to be position assumed by the male and female, in that the male is oriented under the female with his ventral side upward. The only record of such a position is that of Hiatt (1948:199) for a grapsoid crab, *Pachygrapsus crassipes,* and accounts given in this paper for the two species of *Hemigrapsus.* It is quite possible that the Majidae may resemble the Grapsidae in respect to posture, and that the female-over-male position is more common in the Brachyura than the literature would suggest. The many descriptions for the cancroid crabs (Williamson, 1903:101; Hay, 1905:405; Churchill, 1918:105; and others), have fostered the general opinions that (1) crabs copulate in a male-over-female position, and (2) many species copulate in a soft-shell condition. With the more recent literature on crab natural history the general pattern of brachyuran copulation is becoming more well known.

*P. gracilis* was observed *in copulo* both in the Point Defiance laboratory and in the field. All of our observations were made in December and February, but the period of mating is probably not limited to those months for reasons discussed below. In the laboratory pairs were observed under both lighted and darkened conditions. Our records indicate that time of day has no effect on time of copulation, but there is no clear proof of this. Field records were made only at night, while laboratory animals copulating in the day time may have been conditioned to artificial lighting.

In every case the pairs observed in the laboratory were on a level substrate, as the few rocks available to the crabs did not permit them to cling to a vertical surface. In nature all of the animals observed were either on vertical pilings or on vertical rock surfaces. This suggests that either a vertical or horizontal substrate is adequate, but that the vertical is probably used more often. In either case, the body position of copulating pairs is always horizontal. The process of the initiation of copulation was not seen. Pairs observed in nature used the last two pairs of walking legs to hold onto the vertical surface of the substrate, and the chela and first two pairs of walking legs to hold the opposite sex. In one case copulation continued for over an hour after observation began. A pair carefully removed *in copulo* from a piling, in such a way that they could not separate, revealed that the male abdomen is positioned under that of the female and that sperm is transferred by means of the first and second pleopods.

*Pugettia producta*

HABITAT: The kelp crab, *Pugettia producta,* is shown to have a range from British Columbia to Baja California by Garth (1958:188–189). I have seen this species in a multitude of different habitats ranging from open kelp beds off California to unprotected rocky coast, protected rocky coast, and into bays or estuaries. Baker (1912:100) states that at Laguna Beach, California, the young of the kelp crab are very common in tide pools clinging to "*Fucus*" and other brown algae, but mature specimens are only to be found in the kelp beds. Way (1917: 370) found this crab abundant everywhere in the Friday Harbor region in eel grass, on kelp, and on the piles under docks, common to at least 40 fathoms. Other workers generally cite this species as living on kelp, on pilings, or in similar situations. In my experience this species not only uses a broad range of habitats but is seasonal in the micro-habitat that it occupies. On the open coast of California it was commonly found among the rocks or in the shorter species of kelp, such as *Egregia,* during the extreme winter period. In summer the adults migrated to the large floating kelp, leaving only the juveniles in the immediate intertidal zone, as described by Baker. In the Puget Sound area a similar phenomenon is observed in that this species becomes extremely abundant on pilings during the cold parts of winter. The kelp crab is absent from pilings during summer months when the floating kelp, *Nereocystis,* is fully grown and abundant. This crab is also found in summertime feeding amongst drifts of *Sargassum* on a smooth sandy substrate. Whether or not the kelp crab feeds in this manner during wintertime is not known. It is noteworthy, though, that the crabs disappear from pilings during summer months; where one will find a few specimens in summertime, he may find ten to fifteen in wintertime. The chief requirements for the habitat of this species seem to be abundant supplies of fresh water and of food. Being primarily a herbivore, it devours tremendous quantities of brown algae. Juveniles are most frequently found in *Zostera* beds, as cited by Way. Adults are occasionally found there also, but the marine grass does not support the weight of the adult and thus the animals seldom stay within this zone. *P. producta* shows a distinct preference for some type of structure which will enable it to climb up above the substrate, and pilings or the floating kelp are most frequently inhabitated.

FOOD AND FEEDING HABITS: About 15 specimens of *P. producta* were examined to determine their food content. The material in the stomach consisted principally of plant tissue. Members of the brown algae are the primary source of food. Among the most common species of algae are *Fucus, Sargassum, Nereocystis,* and, on occasion, *Ectocarpus.* Small amounts of red algae resembling *Gigartina* spp. and some species of filamentous red algae were also noted. During the extremes of winter, when most of the specimens are found on pilings, the diet of this crab seems to change markedly. In the field large specimens of *Pugettia producta* were engaged in breaking barnacle shells and consuming the tissue inside of the shell. Stomachs examined during this period contained large quantities of barnacle fragments, fragments of the common mussel, *Mytilus edulis,* and also small quantities of hydroids and bryozoans. Apparently this crab becomes quite carnivorous during periods when the large brown algae are absent from its typical habitat.

During feeding operations this species uses the walking legs to hold on to the algae and the chelapeds to cut bits of algae and transfer them to the mouth parts. Large fragments are swallowed whole and are later ground up by the gastric mill within the stomach. When feeding on barnacles the chelapeds are again used. The movable finger is inserted into the open edge of the barnacle and the shell is pried outward, thus breaking the side of the barnacle's case. The shell then becomes dislodged from the piling and the tissue is devoured. Presumably small mussels are broken in a similar manner. In the laboratory one could not help but notice the keen visual awareness of this species as food was placed in the aquarium. Algae and cut fish alike were caught in mid-water as they sank past the crabs. The slightest movement of food seemed to attract the attention of crabs quite some distance away in the tanks. Cut fish that was secretly placed in the tank, however, would go unnoticed for some time. This suggests that sight and the tactile senses are most highly developed for feeding, and that the chemical sense is not very extensively used.

REPRODUCTIVE ACTIVITY: Garth (1958:192), in his discussion of breeding of *P. producta,* states that gravid females were commonly found at Coos Bay, Oregon, in June and July; in Sonoma County, northern California, from October to February; and at Dillon Beach, Marin County, in August and November. In southern California females with ova have been taken from November to February and in lower California in January, March, and June. In our own collecting, field encounter of this species ranged from a few up to about 18 females each month, except during May, September, and October, when we were unable to locate any females of this species. Females carrying eggs were found during every month of the year with the exceptions noted above. Moreover, except in November and December, all females examined each month had eggs. This species seems to be omni-seasonal in its egg production, but there is a trend of egg deposition beginning in November and December and becoming more apparent in the month of January. This is followed by an embryonic development during March, April, and May. Some extremely new eggs are found again in April, July, and August with hatching in August, February, and April. Since none of the field animals observed from month to month were tagged, it would be conjecture to say whether two broods of eggs are produced annually. Laboratory data seem to indicate that the development of a single brood requires the greater part of the year.

PRODUCTIVITY: Eggs within the egg masses of 11 individuals were counted to determine the size of an average brood. The hepatic carapace width of these specimens ranged from 41 mm to 56 mm; and the number of eggs per mass varied from 34,000 to 84,000, with an average of 61,000 eggs per brood. New eggs are bright orange and progress to a very deep red before part of the embryo becomes hyaline and deep purple. At this time the eyes begin to show and there is a reduction in the amount of purple material within the egg case. The egg mass appears somewhat grayish-purple at time of hatching, due to the hyaline interior, eye spots, and purple pigmentation.

COPULATION: At no time was the process of courtship and/or copulation observed for *P. producta.* The process is probably similar to that as described for *P. gracilis.* On several occasions in the field we observed what appeared to be the onset of copulation: pairs of *Pugettia producta* were seen on pilings, going through a wrestling motion which resembled the beginning of copulation. The animals were situated with one individual above the other, each facing the other. Repeatedly, as we continued to observe this process, the lowering tide would interrupt the activity. The pair would then move farther down on the piling and resume this "grappling" motion, but before copulation could begin the tide would again interrupt. The pair was finally forced to leave the piling and move out on the sandy substrate. These animals probably copulate either on pilings or on the large bladder kelp at night, but are probably more secretive about it than other species.

*Oregonia gracilis*

HABITAT: The decorator crab, *Oregonia gracilis,* ranges from Bristol Bay, Alaska, to Monterey Bay, California, and from the intertidal zone down to depths of 212 fathoms (collected by the Albatross, recorded by Rathbun, 1894: 59). Way (1917:369) records that this animal is quite abundant at all depths down to 55 fathoms, or possibly greater, at Friday Harbor. She cites such areas as the pilings at the Friday Harbor dock, eel grass off Browns Island, and along various beaches in the San Juan Island chain. While the general nature of the habitat in southern Puget Sound seems to be similar to that recorded by Way, the crabs can not be considered as abundant. Adult forms were scarce indeed, and considerable effort was required to find even one or two individuals during the winter season on the pilings. The fact that these crabs are so highly decorated and that they choose to live amongst algae and invertebrate-encrusted pilings may mean that their presence was simply less noticeable. Adults were found chiefly on pilings or on sea walls, while juveniles were more frequently found on *Zostera.* Due to the lack of individuals our records are extremely weak for this species and we have made no all-out attempt to study its reproductive cycle. We will present those data that are available to make the record as complete as possible.

REPRODUCTIVE ACTIVITY: Data concerning reproductive activity for *O. gracilis* seem to be scarce and incomplete. Rathbun (1925:73–78) records ovigerous females from St. George Island, Pribilof Islands, in May and September; from Attu Island and Petral Bank, Aleutian Islands, in June; for Cordova and Yes Bay, southeastern Alaska, in June and August, respectively; and from Comox, Vancouver Island, British Columbia, in July. Garth (1958:139) records as gravid 25 of 40 females taken in late July, and 20 of 40 females taken in early August in the San Juan Strait–Puget Sound region. One specimen collected at Point Defiance in October, three collected there in December, and one collected in February were ovigerous. The eggs for these months were of a new, bright red nature. The summertime records of both Rathbun and Garth should not be interpreted as meaning that females are most frequently ovigerous during that season for, by consulting Rathbun's many station records, one may see that all occurred during the late spring and summer months and none were made between October and April. Those few specimens of *O. gracilis* maintained at the Point Defiance aquarium behaved like the other species of spider crabs cited above: that is, eggs were carried over the major part of the year and development was quite slow, with hatching occurring after irregular intervals.

PRODUCTIVITY: Three specimens, sacrificed for ova counts, ranged in carapace width from 17 mm up to 25 mm. The number of eggs ranged from 2,800 up to 17,400, with an average of 9,200 eggs per brood. Data are too few to suggest that only one brood is produced per year, although this is probably the case. Observations of other reproductive activity such as courtship, copulation, and egg deposition are wanting.

*Scyra acutifrons*

HABITAT: The sharp-nosed crab, *Scyra acutifrons,* is recorded from Kodiak Island, Alaska, to San Diego, California, and from the intertidal zone down to 40 fathoms (Rathbun, 1910: 175; 1925:196), and down to 55 fathoms by Way (1917:371). The writer recalls having taken this species north of the published range in the Cook Inlet area in Katchemac Bay, while doing king crab research in the summers of 1957 and 1958.

This species was taken only in two situations in southern Puget Sound: first, on pilings where barnacles were extremely numerous, and, second, on rocks in areas where strong currents prevailed during changing of the tide. Way suggests that this species is not abundant, and this was surely our own experience. We did not find it within *Zostera* beds, and only on one occasion was it found moving across an open sandy substrate. The crabs are often decorated with bits of sponge, hydroids or other invertebrates, or bits of algae, and generally match the surroundings of pilings or rocks very closely. Like the other species of spider crabs, *Scyra* attains a position with the anterior end pointing downward and thus is very inconspicuous when hiding amongst barnacles on a piling. Frequently the only sign that would allow one to detect the crab was the tiny amount of coloring between the pinching fingers of the chelapeds. From our collecting and our field impressions we would say that this species is definitely more abundant in December and January than in the spring and summer months. However, it is also true that during these cold-water months the algae are practically absent from the pilings. Thus this crab is probably more readily observed in the absence of algae or other invertebrates.

REPRODUCTIVE ACTIVITY: The nature of the hiding places used by *S. acutifrons* has made observation of reproductive activity, other than the possession of eggs by females, difficult to observe. Garth (1958:255) records collecting ovigerous females off southern California in every month but March, July, and September; and Way (1917:371) records taking two ovigerous females in July at Friday Harbor, Washington. Ovigerous females were collected or observed during every month except April and May and September and October, when no specimens of *Scyra* were collected at all. There is no doubt that ovigerous females do occur during these "barren" months, since females with very new eggs were found just prior to these times. Moreover, females with extremely new eggs were collected during all of those months cited above and hatching was witnessed in the months of December and January, and June, July, and August. Results of 2 months of collecting will give an idea of the egg development encountered during different months of the year. During July, 12 of 17 females were ovigerous and, of the 12, 8 had extremely new eggs, one was of intermediate development showing eyes, and 3 were in the hatching stage. In December, 29 of 53 were ovigerous, with 25 having extremely new eggs, 3 well-advanced eggs, and one being in the hatching condition. Apparently there is no well-defined season of reproduction that governs periods of quiescence and periods of reproduction, although there is some suggestion that hatching may be confined to June through August and December and January.

PRODUCTIVITY: Eggs in egg masses of 12 specimens of *Scyra* were counted. These specimens ranged from 19.5 mm to 30 mm in carapace width, and the egg mass size ranged from 2,700 eggs to 16,300 eggs, with an average of 8,600 eggs per female per brood. Dissections show that oögenesis occurs while the female has ova attached to the pleopods and thus a second brood may be produced very shortly after the current brood has hatched.

### FAMILY PORCELLANIDAE

*Petrolisthes eriomerus*

HABITAT: *Petrolisthes eriomerus* may be found in abundance in certain localities within the southern Puget Sound area. It was collected in large numbers in the Tacoma Narrows and at the Port Orchard collecting site. Smaller numbers were collected and observed at the eastern end of Titlow Beach and few specimens were observed at Point Defiance. Workers who have described the habitat of this animal consistently mention that they are found under rocks in the intertidal zone (Way, 1917:350; Hart, 1930:105). Haig (1960:76) states that this crab occurs under stones in the lower part of the tidal zone in the northern part of the range, south to San Luis Obispo County, California. Both Way and Haig cite some deep collecting records for this species, but these records are predominantly for the southern extreme of the range, suggesting that isothermic temperature may be a partial key to the habitat of this crab.

One habitat characteristic must always be present when these animals are to be found: there must be some current, however strong, which will bathe the habitat and will supply it with fresh plankton which is the chief source of food for this species. In all cases the number of specimens seemed proportional to the swiftness of the current. The effect of a swift current on the habitat may be manifold: water is removed, food is carried into the habitat, and excessive debris is removed from the undersides of rocks. *P. eriomerus* is commonly seen clinging to the underside of rocks with its ventral side up towards the rock surface. When rocks are turned over numerous specimens are found clinging to the bottom. This species typically lives and feeds in this inverted position, using the tarsal hooks for holding onto rocks, or for locomotion. Without the protection of rocks these crabs right themselves and walk about on a sandy substrate in a normal manner. When these animals are dislodged and dropped into water they use the abdomen for locomotion.

They swim by trailing their front chelae and flapping their abdomens, thus propelling themselves backward through the water.

FEEDING HABITS: More than 20 specimens of *P. eriomerus* were examined microscopically to determine the nature of the stomach content. As all of the contents seemed quite similar, detailed notes were kept only for 10 individuals. The majority of stomachs contained almost pure masses of diatoms. Only one contained sessile diatoms found growing on the rocks within the *Petrolisthes* habitat. The others contained diatoms of a pelagic form. Two or three had extremely large fragments (up to 1 mm long) of some species of green algae. From the gut content alone it seems that this animal is predominantly a filter feeder, though evidence shows that some cropping of sessile algae is carried out also. Observations in the field and in the aquarium show that this species spends most of its time with its ventral surface held against the bottom side of a rock and with the face showing at the edge of the rock where water currents are continuously being sampled. The movement of the mouth parts suggests that this animal filters its food from the water. Laboratory animals, for the most part, refused meat fragments offered to them. This species, then, is thought to stay within the confines of the rock under which it is hiding, and to feed at the periphery of this rock by filtering or by cropping algae growing within chelae reach.

SYNOPSIS OF REPRODUCTIVE ACTIVITY: Figure 7 shows that oögenesis probably begins in the month of October and continues until the time of ovulation, fertilization, and egg deposition. We assume that copulation probably takes place in January. Egg deposition begins in the early part of February and increases rapidly until the early weeks of April, when the majority of females have produced their first brood of eggs. Hatching probably begins around the first of May for the first brood and continues into the first week of August. Egg deposition for brood number two begins about the middle of May and reaches its peak about the early part of August. At this time hatching of brood number two begins and continues into early October. Referring to the physical conditions represented on Figure 7, one could make the suppositions that copulation begins shortly after the shift

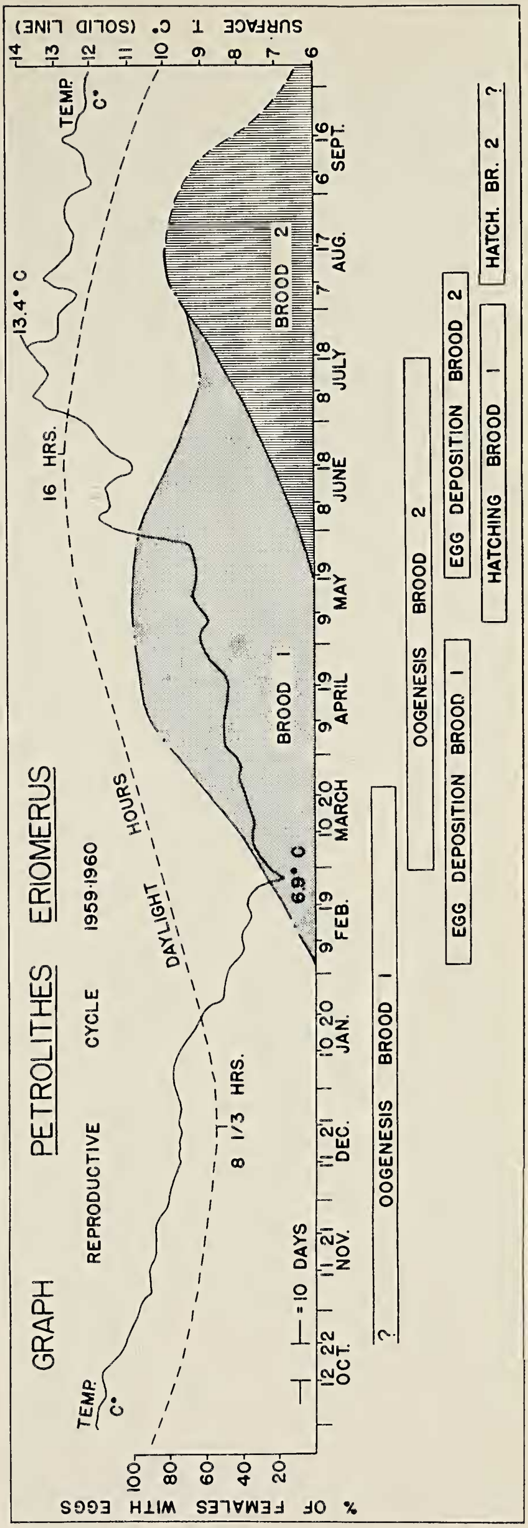



FIG. 7. The reproductive cycle of *Petrolisthes eriomerus.*

from decreasing photo-periods to that of increasing photo-periods; and that there is some correlation between deposition of brood number one and increase in water surface temperature. However, these suppositions need a considerable amount of research to test their validity.

COPULATION: No data as to the time, method, or frequency of copulation were obtained.

OÖGENESIS AND EGG DEPOSITION: The exact time at which oögenesis begins is not known, but a projected curve suggests that it begins in October. By early November some of the ovaries show considerable development of the ova, while others have ova ranging around 0.015 mm in size. However, by the end of November those few specimens examined had ova averaging about 0.35 mm in diameter and bearing a yellow-orange pigment. By the end of January most of the ova measured about 0.68 $\times$ 0.60 mm. Throughout February there is a very slight increase in size until deposition occurs. Figure 7 shows the season of egg deposition for both the first and second broods as far as our data will permit. From the latter part of February until mid-April egg deposition occurs rapidly but then begins to taper off until the middle of May, when over 97% of the females have eggs. Hatching begins toward the end of May and continues until the first week of August, when the last of brood number one hatches. Brood number two begins before the first of June and egg deposition is rapid until the early part of August, when from 74 to 80% of the females carry new eggs. From here a theoretical curve would show that hatching follows very quickly and that brood number two probably is completed by the end of September or the early part of October. It is possible, therefore, that oögenesis may begin again while brood number two is still carried on the pleopods.

PRODUCTIVITY: The number of eggs carried by 37 different females was determined. Carapace length ranged from 6.9 mm to 13.6 mm. Broods ranged from only 10 eggs in the smallest individual to 1,580 in the largest specimen. The average count for 37 individuals was 621 per brood. If each female produced two broods per year, a total of about 1,250 would be produced. Considering that only up to 80% of the females produce a second brood, a more accurate annual production for all females would be about 1,100 eggs per year. The extremely large size of the egg of this species (about 0.75–0.80 mm) demonstrates that a larger larval form is produced, which theoretically could better fend for itself and thus lessen the danger of predation and starvation.

### *Pachycheles rudis*

HABITAT: The habitat of *Pachycheles rudis* is below the minus-zero tide level where water currents are strong, in such places as are listed by Haig (1960:172): under stones, the holdfasts of kelp, in sponge cavities, among rock oysters and mussels, in tunicate beds, and in the discarded burrows of dead burrowing clams. MacGinitie (1935:712) states that males and females live together in pairs. This species was taken on occasion under rocks with *Petrolisthes eriomerus* at the Tacoma Narrows. It was found in great abundance, however, at Port Orchard, in the situations cited by Haig. Most frequently pairs were found within the empty burrows of rock-burrowing clams (*Petricola*). The size of the animals within the burrows often seemed much greater than the outer aperture of the burrow. When the burrows were opened with a geological pick larger specimens seemed unable to escape by means of the normal aperture, or else were reluctant to do so. It is suggested that young pairs occupy these burrows, feed on plankton and grow, reproduce, and continue their existence until they have reached a size much greater than the tapered burrow opening. Specimens brought to the Point Defiance laboratory would occupy any small cavity provided, such as small vials, cones made out of screen wire, and empty shells. Animals removed from these artificial chambers again proved to be in pairs. In the laboratory this species was extremely sensitive to the oxygen content of the water. If the running sea water was shut off within the 30-gal tanks for a period of several hours, death occurred, and increased as time progressed. This species was more sensitive in this respect than the other crab-like Anomura we worked with, and the Anomura in turn proved to be more sensitive than the Brachyura.

REPRODUCTIVE ACTIVITY: Our field records for *P. rudis* from the middle of December through August show that between 75 and 100%

of the females were reproductively active. Egg deposition begins in the middle of December and continues into the spring and early summer. Without a doubt, developing embryos are carried long after the middle of August, although we have no observations for this species from that time on. Data suggest that two or three broods of eggs may be produced each season. The peak of hatching of the first brood is evident in April and May, though it may begin in the last week of March in some individuals. Females carry new, orange colored eggs or "prehatch" eggs (gray and showing eyes) throughout April and May. A study of these animals in the first week of May shows that: (1) almost 100% of the females with prehatch eggs have ovaries swollen with large, bright orange ova which will produce the second brood of offspring; (2) about 50% of the females with new orange eggs attached to the pleopods have ovaries still engorged with bright orange ova which may represent brood two or three; and (3) about 50% of the females with new eggs attached to the pleopods have ovaries holding a few to about a half the normal number of ova in the bright orange, prefertilized state. These data may mean that either some females produce a first or late winter-to-spring brood, a second or spring brood, and a third or summer brood for a total of three broods (usually), or that females produce two broods. In the latter case, some of them would begin with a winter–spring brood and others would begin in the spring, thus giving a staggered timing and a seeming third brood. Our data show all of the females to be ovigerous in late December, thus suggesting three broods, but these data are too few to be more than suggestive. Eight of 16 females encountered during the first week of August had eggs which were classified "almost prehatch," but belonging to the second or new brood, while the remainder of the specimens had extremely new eggs attached to the pleopods. One field datum is of interest here. A single female bearing extremely new eggs was found to have a very soft exoskeleton and had obviously just molted. This suggests that the females may molt prior to extruding the new brood.

PRODUCTIVITY: Fourteen females were preserved and the eggs counted. The carapace width ranged from 12.0 to 16.8 mm, and the number of eggs ranged from 210 to 2,130. The average was 928 eggs per brood. This latter figure is misleading, in one sense, as to the reproductive capacity of *P. rudis.* Of the females representing all size classes, 43% had large clutches of eggs (from 1,175 to 2,130), with an average of 1,555 eggs per female. The remaining 57% had small clutches of eggs (from 210 to 625), with an average of 410 eggs per female. Of the large-brood females, half were with new eggs and half with prehatch eggs attached to the pleopods, while all had ovaries completely swollen with bright orange ova. Of the small brood females (87% with new eggs on the pleopods), 63% had ovaries with some large orange ova, while 37% had ovaries filled with large orange ova. These data support the idea that three broods may be produced by this species each year, but suggest that not all broods are equally large that is, roughly proportional to carapace size, as is true for the Grapsidae and Xanthidae, etc. Rather, any one of the possible three broods may be small or large.

## FAMILY LITHODIDAE

### *Haplogaster mertensii*

HABITAT: *Haplogaster* is not considered to be at all common in the southern Puget Sound area. It was collected only at one locality, the Tacoma Narrows. There, in the swift moving currents, this crab is located under rocks which afford good protection, but provide considerably more room for moving about than would be required by *Petrolisthes eriomerus.* Although in its ecological make-up the Port Orchard collecting site seems to be similar to the Tacoma Narrows, this crab is not found there. These animals were never collected in abundance, eight or nine being a large number for any one trip. With very few exceptions all of the specimens were released at the time of collecting to insure a continuous population for study. It is possible that currents are necessary in this habitat to clean debris from under rocks and thus insure ample space, and to bring food and oxygen to this crab. Experimentation has not been made as to oxygen requirements of this animal, but it seems possible that its restricted distribution may be governed by any of the above factors, not least of all oxygen.

FEEDING HABITS: Whenever it was necessary to sacrifice a specimen of *Haplogaster,* the stomach contents were analyzed (this crab is sufficiently rare in the southern Puget Sound area to justify an extremely conservative use of specimens). Three animals were examined. In the stomach contents fragments of some species of brown algae were fairly common, along with some monofilamentous red algae, and fragments of what appeared to be *Ulva* or some other green algae. One animal contained a large quantity of single diatoms, most of these being extremely small. However, in the laboratory when animals were introduced into the tanks they immediately attacked barnacles attached to the rocks and fed on these by twisting the shell of the barnacle with the chelae and eventually crushing the barnacle. Apparently this species is omnivorous and feeds both by filtering, by gleaning algae attached to rocks, and by breaking barnacle shells to obtain animal tissue. It is not known whether or not this species captures motile forms.

REPRODUCTIVE ACTIVITY: The reproductive activity of *H. mertensii* remains a mystery for the most part, because of its scarcity in southern Puget Sound waters and the difficulty of feeding and maintaining it under proper environmental conditions over long periods of time in the laboratory. The few data obtained are of value, however. With only one exception, every female encountered in the field during the latter part of November, December, January, and April had developing embryos attached to the pleopods (tides during February and March were unsuitable for obtaining *Haplogaster*). Eyes within the egg shell became evident during the month of January, and hatching occurred in the laboratory and in the field during the middle part of April. Females observed during June and July were without eggs attached to the pleopods, and no further observations were made until the latter part of November and early part of December, when females again carried eggs.

PRODUCTIVITY: Three females were preserved and their eggs were counted. The carapace width and the number of eggs borne by these specimens are as follows: (1) carapace 15.6 mm, 600 eggs; (2) carapace 18.0 mm, 2,076 eggs; (3) carapace 19.1 mm, 2,070 eggs.

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